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MECHANISMS OF RIPARIAN PLANT COMMUNITY ORGANIZATION AND SUCCESSION IN THE GRAND CANYON, ARIZONA

By

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ABSTRACT

MECHANISMS OF RIPARIAN PLANT COMMUNITY ORGANIZATION AND SUCCESSION
IN THE GRAND CANYON, ARIZONA

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Abiotic and biotic mechanisms influencing perennial riparian plant
community structure and succession in the Colorado River riparian
corridor in Grand Canyon National Park were examined through field
surveys and field, nursery and laboratory experiments.   Factors
investigated included the impacts of flooding disturbance, interspecific
competition, and dam-induced edaphic changes on germination, growth and
recruitment of riparian perennial plant species. [Evaluation of 3
hypotheses on disturbance, competition and adaptation demonstrated
conditional community responses based on adaptation to gradients.
Experiments on the role of interspecific competition in the successional
displacement of exotic Tamarix ramosissima by native Salix exigua
demonstrated that direct asymmetric competition only occurred between
seedlings; however, indirect (exploitative, mechanical) responses
inhibited colonization of Tamarix stands by non-clonal native species.
Experimental studies demonstrated that reduced recruitment of riparian
plant species was attributed to dam-induced alteration of substrate
quality, with increased selection against species with low allocational
phenotypic plasticity.

ii

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Riparian ecosystems, including wetlands, are the most biologically productive and the most poorly managed terrestrial habitats in the American Southwest (Johnson and Jones 1977; Warner and Hendrix 1984; Johnson et al. 1985; Mitsch and Gosselink 1986). Despite the biological and economic importance of riparian habitats, the role and relevance of ecological factors regulating riparian plant community organization have not been systematically investigated. Flooding disturbance, dam-modified discharge regimes, moisture availability, substrate texture, temperature, and the potential for biotic influence (e.g. competition and herbivory) on riparian plant community structure are among the most readily apparent of these factors. The present study was undertaken to elucidate the ecological mechanisms responsible for riparian plant community structure in the unregulated tributaries and regulated mainstream of the Colorado River in Grand Canyon National Park, Arizona.

Literature Review

Factors Influencing Plant Community Organization

Plant community structure is regulated by spatially and temporally variable abiotic and biotic gradients that constitute a multi-dimensional selection matrix in which only adequately adapted individuals and populations may survive (Watt 1947; Whittaker 1967; Harper 1977; Whittaker and Levin 1977; Grime 1979; Spence 1982; Sousa

1

1984; Schmida and Milson 1985; Tilman 1988). Abiotic gradients held responsible for plant community structure include: disturbance (Levin and Paine 1974; Connell 1978; White 1979; Sousa 1979a, 1984; Atgugov 1982; Miller 1982; Canham and Marks 1985; Pickett and White 1985; Day et al. 1988; Goldberg and Gross 1988); moisture availability (Johnson et al. 1976; Clark and Benforado 1981; Brotherson et al. 1985; Anderson and Warren 1985; Fowler 1986; Welling et al. 1988); nutrient availability (Mitsch and Gosselink 1986; Tilman 1985, 1988; Lajtha and Schlessinger 1988); light availability (Harper 1977; Derlin 1988); stress tolerance (Hosner 1960; Stevens and Waring 1985); and habitat heterogeneity (Whittaker and Levin 1977; Gross and Werner 1982; Harrison and Werner 1984). The study of plant community structure has been advanced by consideration of interaction effects between gradients (Grime 1977; Connell 1978; Noble and Slayter 1980; Menge and Sutherland 1987), predation or herbivory (Paine and Vadas 1969), resource availability (Grime 1977; Tilman 1985; Mitsch and Gosselink 1986), and adaptation of constituent species to those gradients (Grubb 1977; Nilsen et al 1984; Sousa 1984; Canham and Marks 1985; Huston and Smith 1987).

Abiotic (Factors.) Disturbances influencing plant communities include fire, windstorms, flooding, earthquakes and slope failures, volcanism and other natural disturbances (White 1979; Sousa 1984), as well as innumerable anthropogenic disruptions, such as deforestation, agricultural practices, grazing, mining spoils (Antonovics and Bradshaw 1970), urbanization, thermal and other forms of pollution (Muzika et al. 1987), stream channel modification and river impoundment (Water Science and Technology Board 1987). Flooding is a ubiquitous form of

disturbance in unregulated riparian environments, particularly in the arid Southwest where scouring spates remove mature plants and open patches of riverbank habitat required for for seedling establishment (Horton et al. 1960; Campbell and Green 1968; Warren and Turner 1975; Fenner et al. 1984; Reichenbacher 1984; Stevens and Waring 1988). Flooding effects vary spatially, increasing in intensity with proximity to the channel (Hereford 1984; Kozlowski 1984; Webb et al. 1987; Stevens and Waring 1985), as well as temporally. Riparian vegetation is characterized by strong patterns of zonation parallel to the channel (Johnson et al. 1976; Carothers et al. 1979; Turner and Karpiscak 1980; Nilsson 1985; Spence 1982; Mitsch and Gosselink 1986), with flooding or soil gradients usually ascribed as mechanisms (Campbell and Green 1968; Brotherson 1987). The "intermediate disturbance hypothesis" (IDH) of Paine and Vadas (1967), Horn (1974,1975), Connell (1978) and Sousa (1979a) predicted that the number of species (S) in a habitat should be highest where ecological disturbance was intermediate in intensity.

Numerous other abiotic gradients regulate plant community structure in arid systems. The influence of moisture availability has been well-documented (Whittaker and Niering 1965). Nutrient availability has been ✳ considered dependent on moisture availability (Fowler 1986), and Grime (1979) and Tilman (1988) predicted that decreasing productivity (decreasing resource availability) would result in a shift in species compostition towards a community more tolerant of low nutrient availability. Interaction between disturbance and substrate gradients were considered important in studies by Nanson and Beach (1977), Spence (1982) and Reichenbacher (1984). Changes in gradients or establishment success through time are generally held responsible for succession

(Crocker and Major 1955; Loucks 1970; Drury and Nisbet 1973; Connell and Slatyer 1977).

Biotic Gradients. Biotic gradients held responsible for species distributions and plant community structure include: competition (Trenbath 1974; Schoener 1983; Lajtha and Schlessinger 1988); predation, mutualism (Atsatt and O'Dowd 1976: Acher 1988); as well as the adaptive significance of various life history traits, including phenology, dispersal, germination and establishment criteria (Horton et al. 1960; Warren and Turner 1975; Grubb 1977; Noble and Slatyer 1980; Sousa 1984; Fenner et al. 1984; Canham and Marks 1985; Asplund and Gooch 1988); and mutualism (Atsatt and O'Dowd 1976; Archer et al. 1988).

Interspecific competition has been ascribed an important role in plant community organization and succession (Watt 1947; Connell and Slatyer 1977; Harper 1977; Grubb 1977; Grime 1979; Grime and Hodgson 1987; Huston and Smith 1987; Menge and Sutherland 1987). Two general forms of competition (Schoener 1983) may serve as mechanisms in the three models of community succession described by Connell and Slatyer (1977). These forms of competition include indirect exploitation (e.g. preemption and consumption of resources), and direct interference competition (e.g. allelochemical interaction. Experimental data demonstrating direct interspecific competition among plants are abundant (de Wit 1960; de Wit et al. 1966; Trenbath 1974; Harper 1977; Connell 1983; Schoener 1983); however, pairwise comparisons of species, particularly in laboratory settings, have occasionally lead to rather inappropriate conclusions for complicated field situations involving a multitude of species (e.g., Kroh and Stephenson 1980). The several form(s) and relevance of interspecific competition probably vary between

systems, and have remained largely untested. Interspecific competition has been considered most influential in highly productive, ecologically stable environments (Weins 1977; Connell 1978; Grime and Hodgson 1987). Studies examining the form(s) and importance of interspecific competitive interactions are required if we are to understand the role of competition in succession (Drury and Nisbett 1973).

The intensity of herbivory has been found to be positively correlated with moisture availability and, were herbivory a determinant of riparian vegetation structure, it should diminish species richness, density, and cover of plant species to a greater degree at the water's edge. Stevens (1985) found that levels of invertebrate and vertebrate herbivory were higher on plants near the water's edge than on drier, low disturbance terraces, but that herbivory was of minor consequence to growth of two dominant riparian plant species (Tamarix ramosissima and Salix exigua) along the Colorado River in the Grand Canyon.

Riparian Vegetation

Despite mounting scientific and political concern over mismanagement of riparian habitat, understanding of the evolution and ecology of riparian vegetation has been limited to studies which concluded, without experimental evidence, that riparian plant community structure was ascribed to flooding disturbance and fluvial geomorphology (e.g. Campbell and Green 1968; Irving and West 1976; Asplund and Gooch 1988). An understanding of the mechanisms governing recruitment and the pronounced pattern of zonation is clearly needed. Also, riparian vegetation presents interesting challenges in biogeography. Riparian habitat occurs in extremely long, narrow belts, an "island" shape which is not treated in biogeographical theory. Such a patch shape must be

subject to considerable "passive sampling" and high rates of extinction. This subject deserves further theoretical attention.

Desertification of the American Southwest is believed to have begun in late Tertiary and Quaternary time and natural selection pressures acting on riparian plant progenitors have doubtlessly increased during the latter half of the Cenozoic Era (Reichenbacher 1984; Axelrod and Raven 1985). The Holocene dendrochronological climatic record demonstrated that desertification has been a punctuated by irregular periods of drought (Euler et al. 1979). In historic times drought was responsible for local dewatering of aquifers and drying up normally perennial tributaries of the Colorado River in Grand Canyon (e.g. Vasey's Paradise Spring in 1977, pers. obs.). The biological productivity of riparian environments has conferred a selective advantage to phreatophyte species exhibiting adaptations associated with increased reproductive and dispersal efficiency, rather than increased drought stress tolerance. Modern xerophytes, on the other hand, have little tolerance of flooding (Stevens and Waring 1985). No native plant species was found to be well adapted to both inundation and desiccation selection regimes simultaneously, although exotic Tamarix ramosissima and native Brickellia longifolia appeared better adapted to both desiccation and inundation (Stevens and Waring 1988).

Succession

Three models of community succession presented by Connell and Slayter (1977) included "facilitation" (a primary succession model), "tolerance" and "inhibition". In the former two models, replacement of early successional species by late succession species was accomplished through interspecific competition, while in the former niche preemption

by early successional species was disrupted by disturbance, with succession only as a consequence of disturbance. Sousa (1979b) disputed the non-competitive mechanism of species replacement in the "inhibition" model, finding that competition, not disturbance, resulted in mortality of colonizing algal species. Furthermore, niche preemption was defined by Schoener (1983) as a specific form of exploitative (indirect) competition. Huston and Smith (1987) assumed competition was universal among plants and broadened the scope of Connell and Slatyer's (1977) discussion by recognizing that all three mechanisms affect individual plants to a varying degree. Thus interspecific competition may serve as a mechanism in any of the three successional models.

Failure of some component(s) of a sessile species' life history strategy may result in its successional displacement in a community (Watt 1947; Drury and Nisbet 1973; Bazzaz 1979; Horn 1974; Connell and Slayter 1977). Riparian vegetation along unregulated streams exists in a state of "suspended succession" in which periodic (often annual) flooding limits survivorship and recruitment (Campbell and Green 1968; Londo 1975; Irving and West 1977; Van Hylckama 1979; Chaghtai and Khattak 1983; Stevens and Waring 1988). Riparian plant recruitment is regarded as a probablilistic function of "safe site" availability (sensu Harper 1977), juvenile or seedling establishment criteria and growth, as well as adult fecundity, abundance and parental investment strategies. Therefore the role of adaptation by constituent species may play a great role in successional dynamics (Nobel and Slayter 1980; Pickett et al. 1988).

Flooding Disturbance and River Regulation

Flooding is the most common form of disturbance in riparian environments, particularly in unregulated streams in the arid American Southwest where scouring spates limit plant establishment along riverbanks (Horton et al. 1960; Campbell and Green 1968; Warren and Turner 1975; Turner and Karpiscak 1980; Fenner et al. 1984; Kozlowski 1984; Stevens and Waring 1985). The scouring effects of flooding constitute a spatial disturbance gradient which increases in intensity with proximity to the channel (Hereford 1984; Webb 1987; Stevens and Waring 1985). Large dams may reduce flooding disturbance of the riparian environment in downstream reaches (Stanford and Ward 1979; Turner and Karpiscak 1980; Howard and Dolan 1981; Petts 1984; Lillihammer and Saltveit 1985), and regulated rivers can be treated as (albeit poorly controlled) experiments in which the effects of reduced disturbance can be evaluated on riparian vegetation. Studies of river impoundment and flood control have revealed the importance of ancillary factors that govern riparian vegetation development, such as erosion and soil change (Pucharelli 1988; Stevens and Waring 1988). Accurate pre-impoundment data and comparative investigation of unregulated tributaries may be used to test the effects of disturbance mitigation on plant community composition and structure.

Because the predicted longevity of large dams may reach 10^3 years large dams create novel evolutionary conditions in which hundreds of generations of plants become estalished in relatively stable and biologically more interactive habitats. For example, the unpredictability of germination sites in unregulated riparian systems should confer a strong selective advantage on species with greater

phenotypic plasticity of germination requirements and seedling growth characteristics (Levins 1962, 1968; Lowell 1985; Schlichting 1986), while the selective value of such adaptation may be lower in regulated riparian environments.

Study Area

I examined the distribution of perennial riparian plants in the ephemeral (dry) and perennial (wet) tributaries, springs, and in the dam-controlled mainstream of the Colorado River in Grand Canyon National Park. The Grand Canyon was selected for this study because: 1) it is the only large riparian system in the American Southwest that has not been subjected to extensive grazing by cattle; 2) it contains a great diversity of riparian systems, including unregulated intermittent and perennial tributaries and springs, and the regulated Colorado River; 3) an excellent historical record has been preserved through photographs of this system since the late nineteenth century; and 4) the hydrology, biota and effects of regulated discharge have received considerable attention, particularly since the mid-1970's (Carothers and Aitchison 1976; Carothers et al. 1979; Water Sci. Tech. Board 1987).

History of Discharge Management in the Grand Canyon

Regulation of the Colorado River upstream from the Grand Canyon eliminated annual flooding events and permitted primary colonization of Colorado River channel margin deposits by riparian plant species (Turner and Karpiscak 1980). Three phases in the discharge regime were recognized in this system (Schmidt et al. in press): 1) the pre-dam era, prior to 1963; 2) the reservoir filling phase from 1963 to 1980; and 3) the post-filling phase. The pre-dam Colorado River in the Grand

Canyon was characterized by high within-year and between-year variation in flow, sediment transport (Howard and Dolan 1981) and water temperature. Virtually no riparian vegetation existed along the river banks below the approximate 2,000 m^3/sec stage prior to impoundment, but was restricted to higher stages and to tributaries (Clover and Jotter 1944, Turner and Karpiscak 1980).

The Filling Phase. Glen Canyon Dam was completed in 1963 and Lake Powell filled from 1963 to 1980. Discharge during the filling phase was far less variable, only exceeding 1,410m^3/sec twice (1965 and 1980). Conspicuous effects of impoundment during the filling phase included: 1) flood control; 2) sediment trapping by Lake Powell, which greatly reduced sediment transport through the Grand Canyon and promoted erosion of some riverside beaches (Howard and Dolan 1980); and 3) a decrease in the mean and variance of water temperature attributed to hypolimnial release. The ecological stability afforded by relatively constant, non-fluctuating flows during the filling phase permitted exotic and native riparian plant life to colonize the previously flood-scoured riverside (Turner and Karpiscak 1980) down to the approximte 1,000 m^3/sec stage. This profuse growth of riparian vegetation presently constitutes the longest stretch of riparian habitat in the western United States and has been widely recognized for its biological and recreational value in an otherwise inhospitable, desert canyon (Carothers and Aitchison 1976; Carothers et al. 1979; Stevens 1976a, b; Turner and Karpiscak 1980; Stevens 1987; Stevens and Waring 1985, 1988; Phillips et al. 1987; Anderson and Ruffner 1988; Brown 1988; Warren and Schwalbe 1985). Increased plant species richness during the filling phase may have been attributed to 1) increasing the colonization rates of native

species because of lower initial population size and/or differential propagule dispersion; 2) differential growth rates and survivorship because of environmental stress, competition, herbivory, or disease; 3) differential growth strategies; 4) alteration of substrates towards nutrient depletion and decreased moisture retention; or 5) lack of "safe" germination sites (sensu Harper 1977).

Riparian succession has continued in this system: exotic Tamarix was the first riparian perennial plant species to become widely established in the newly created riparian habitat, and was common by 1973 (P. Martin pers. comm.; Turner and Karpiscak 1980). More recently, native perennial species, particularly clonal Salix exigua and Tessaria sericea, and Baccharis spp., have colonized the river corridor and have begun to invade habitat formerly dominated by tamarisk (P. Martin pers. comm.; Turner and Karpiscak 1980; Brian 1982; Stevens and Waring 1985; Phillips et al. 1987). Carothers et al. (1979) described the pronounced zonation pattern of riparian vegetation along the Colorado River in this system but did not examine causative mechanisms. The replacement of tamarisk by native species in this system is of considerable interest because the exotic has been a widespread invader of southwestern riparian habitat and is considered to be of limited biological value (Anderson and Ohmart 1979, Johnson 1985; for exceptions see Brown et al. 1984, Brotherson 1987).

The Post-filling Phase. The post-filling phase began when Lake Powell reached maximum stage in 1980. The reservoir was kept at a full stage during in the spring of 1983 and 1984 when record spring precipitation exceeded reservoir capacity and flooded the river corridor in the Grand Canyon. Stevens and Waring (1985) and Stevens and Waring (1988)

concluded that post-dam flooding in 1983-84 <u>significantly reduced</u> ⌐
<u>riparian soil base cation and nutrient concentratio</u>ns, <u>decreased organic</u> ⌐
<u>content</u>, and <u>increased particle size of riverside substrat</u>es, as ⌐
compared to the pre-1983 data of Scala (1984). The percent fine (silt
and clay) fraction of beach soils was found to increase with distance
from the dam, presumably in response to inclusion of tributary-derived
silts. In addition to extensive mortality of mature riparian plants
during 1983-1984 flooding events, Stevens and Waring (1985) reported:
1) extensive germination and recruitment of riparian perennials on fine
(silt-rich) riparian soils; and 2) rapid recolonization of coarser
(sand-rich) beach soils by clonal species which reinvaded beaches from
the protected beach/talus slope interface. Waring and Stevens (1988)
experimentally demonstrated that for three species of riparian
perennials, one month old seedlings were significantly more susceptible
to flooding disturbance effects than were 6 month old seedlings.

From 1986 to 1988 the discharge regime of Glen Canyon Dam returned
to low magnitude daily fluctuations in response to hydroelectric power
demands. Extensive tributary flooding in 1987 and 1988 contributed
significant quantities of fine sediments to beaches in wide reaches of
the Colorado River (e.g. lower Marble Canyon), and significant
aggradation has been reported (J. Schmidt pers. comm.).

The following chapters have been individually prepared for
publication, thus relevant introductory comments and methods are
discussed in each chapter. In Chapter 5 I present a summary and
integration of conclusions drawn from these separate studies.

CHAPTER 2

RIPARIAN PLANT COMMUNITY STRUCTURE: A TEST OF "INTERMEDIATE DISTURBANCE" VERSUS "GRADIENT INTERACTION/ADAPTATION" HYPOTHESES

Introduction

The study of plant community structure has been advanced by consideration of interaction effects between disturbance and other gradients, such as competition (Grime 1977; Connell 1978; Noble and Slayter 1980; Menge and Sutherland 1987), predation or herbivory (Paine and Vadas 1969; Lubchenko 1978), resource availability (Grime 1977, 1979; Tilman 1985, 1988), and adaptation of constituent species to those gradients (Grubb 1977; Sousa 1984; Canham and Marks 1985; Huston and Smith 1987). However, the nomothetic value of hypotheses generated by many studies has been confounded by failure to identify critical gradients affecting a system and/or a lack of appreciation for adaptation to those gradients. The intermediate disturbance hypothesis (IDH, Connell 1978) predicted that maximum species richness of sessile organisms occurred at intermediate levels of disturbance because high disturbance reduced species richness, while competition reduced species richness under low levels of disturbance (Figure 2.1A). Connell (1978) supported the IDH with evidence from coral reefs and tropical rain forests; however, significant desiccation (Sousa 1979a), water depth (Huston 1985 with coral) and/or herbivory effects (Lubchenko 1978) also influenced community structure in those kinds of systems, as did

A.

B.
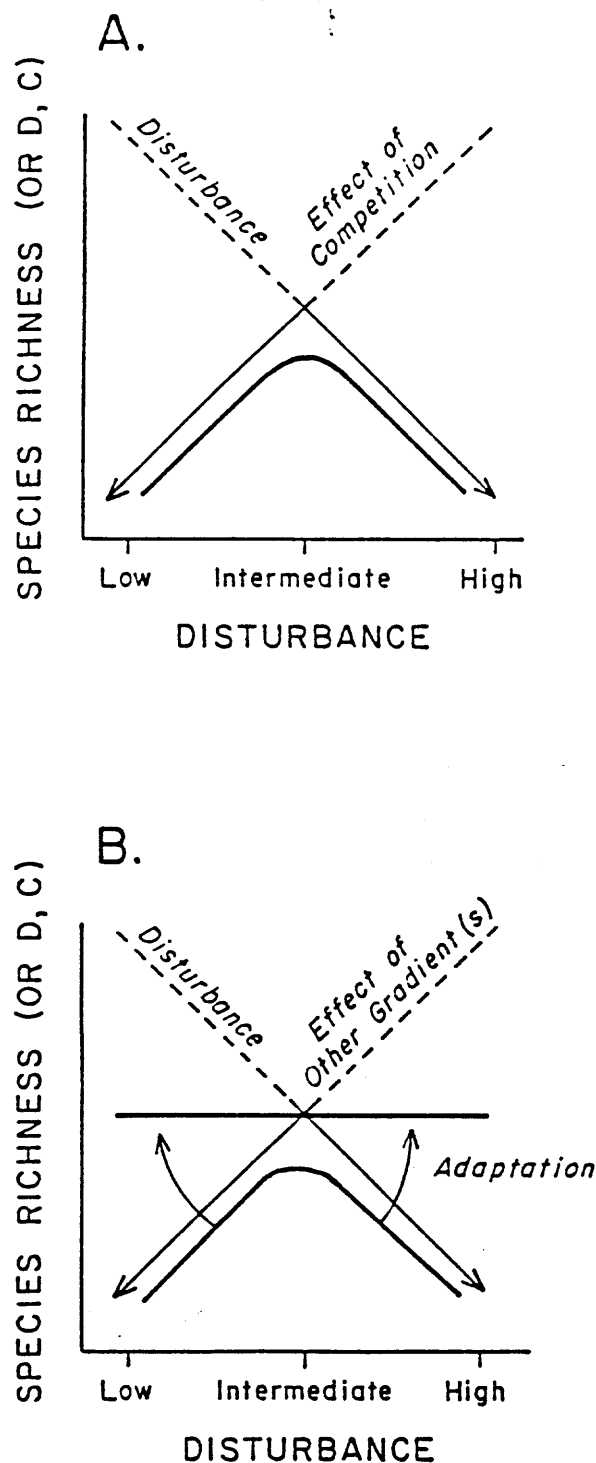
Figure 2.1: Species richness (S), stem density/m2 (D) and basal area in cm2/m2 (C) riparian perennial community responses as a function of varying levels of disturbance (low to high), for the intermediate disturbance hypothesis (disturbance/competition hypothesis) of Connell, 1978 (A) and the gradients/adaptation hypothesis (B). See the text for discussion of these hypotheses.

adaptation by constituent species (Denslow 1980). Diversity is comprised of other community responses to gradients in addition to species richness (S), including density (D) and biological contribution (C as basal area, canopy cover, biomass, volume) of constituent species (Rickleffs 1979). The latter two variables may also be negatively correlated with disturbance and may be influenced by competition (e.g. Nanson and Beach 1977; Sousa 1979a).

Flooding is a ubiquitous form of disturbance in unregulated riparian environments, particularly in the arid Southwest where scouring spates remove mature plants and open patches of riverbank habitat required for seedling establishment (Horton et al. 1960; Campbell and Green 1968; Warren and Turner 1975; Fenner et al. 1984; Reichenbacher 1984; Stevens and Waring 1988). Flooding effects vary spatially, increasing in intensity with proximity to the channel, as well as temporally (Hereford 1984; Kozlowski 1984; Webb et al. 1987; Stevens and Waring 1985). Riparian vegetation structure is typified by strong patterns of zonation parallel to the channel (Brotherson et al. 1985; Carothers et al. 1979; Turner and Karpiscak 1980; Nilsson 1985; Mitsch and Gosselink 1986), with flooding or soil gradients ascribed as responsible factors (Campbell and Green 1968; Brotherson 1987). By reducing flooding in downstream reaches, large impoundments impose ecological stability on non-equilibrium river systems (Turner and Karpiscak 1980; Howard and Dolan 1980; Petts 1984; Lillihammer and Saltveit 1985). River impoundment and flood control studies revealed the importance of abiotic factors other than flooding that regulate riparian vegetation structure, particularly moisture availability (Johnson et al. 1976; Turner and Karpiscak 1980; Pucharelli 1988).

I evaluated riparian plant community adaptations and responses (S, D and C) to interaction between flooding disturbance, competition, moisture availability and other critical gradients along intermittent (ephemeral, dry) and perennial (permanent, wet) tributaries, spring courses, and the dam-controlled mainstream of the Colorado River in Grand Canyon National Park, Arizona. This system was ideal for study because: 1) it offered a diverse array of unregulated tributaries, springs, and dam-regulated Colorado River corridor riparian settings; 2) the relationships between short-term and long-term climatic conditions and flood frequency for major tributaries and the mainstream have been studied in detail (Hereford 1984; Webb et al. 1987; Schmidt and Graf 1988); 3) dam-related riparian vegetation changes in plant zonation along the Colorado River have been well-documented from historical photographs and surveys (Carothers et al. 1979; Turner and Karpiscak 1980); and 4) the Grand Canyon protected the only large riparian system in the American Southwest that has not been severely overgrazed by cattle. The present study was, to my knowledge, the first test of hypotheses on the role of spatial flooding disturbance gradients on perennial riparian plant community structure.

Community response curves (Figure 2.1) were generated for S, D and C in each riparian setting to test two hypotheses. 1) The "intermediate disturbance hypothesis" (IDH) or "disturbance/competition hypothesis" of Paine and Vadas (1969), Horn (1974,1975) and Connell (1978) predicted that the number of sessile species in a habitat should be highest where the effects of ecological disturbance and competition were intermediate in intensity (Figure 2.1A). Because ecological disturbances vary with respect to duration, frequency and magnitude (Sousa 1984), the symmetry

of the community response curve could shift laterally but maximum S should be maintained at some intermediate disturbance level (Miller 1982). The IDH ignored the significance of other gradients and the issue of adaptation to gradients. Thus failure to observe the IDH community response curve where disturbance effects were significant could be attributed to: a) lack of importance of competition; b) non-parallelism between competition, resource availability, predation, or other gradients; c) significant interaction effects between these gradients; and/or d) adaptation by constituent species to critical gradients or gradient interactions. 2) The "gradients/adaptation hypothesis", proposed here, predicted that species richness and other community characteristics may be regulated by critical gradients and gradient interactions, and species may be adapted to the typical range of variation in disturbance and/or other critical gradients in their environment. Even when disturbance effects are strong, species richness or other community responses could increase at either or both ends of the community response curve (Figure 2.1B).

In all, 9 possible plant community response curves may be generated in response to three levels of disturbance and other critical gradients for species richness. These are illustrated and discussed in Figure 2.2.

Methods

Vegetation community characteristics were evaluated on three flood terraces in 85 (64.9%) of the named tributaries of the Colorado River in Grand Canyon National Park between Lees Ferry (River Kilometer = RK 0) and Diamond Creek (RK 364; Stevens 1987) in Arizona. Only tributaries with nontechnical climbing access from the Colorado River and/or channel

COMMUNITY RESPONSE (S,D,C)

I A

I B
S_I S_R

I C

II A
S_X

II B
2
S_P D_X C_X
1
D_I D_R

II C
C_I C_R

III A

III B
D_P C_P

III C

LOW ——→ HIGH   LOW ——→ HIGH   LOW ——→ HIGH
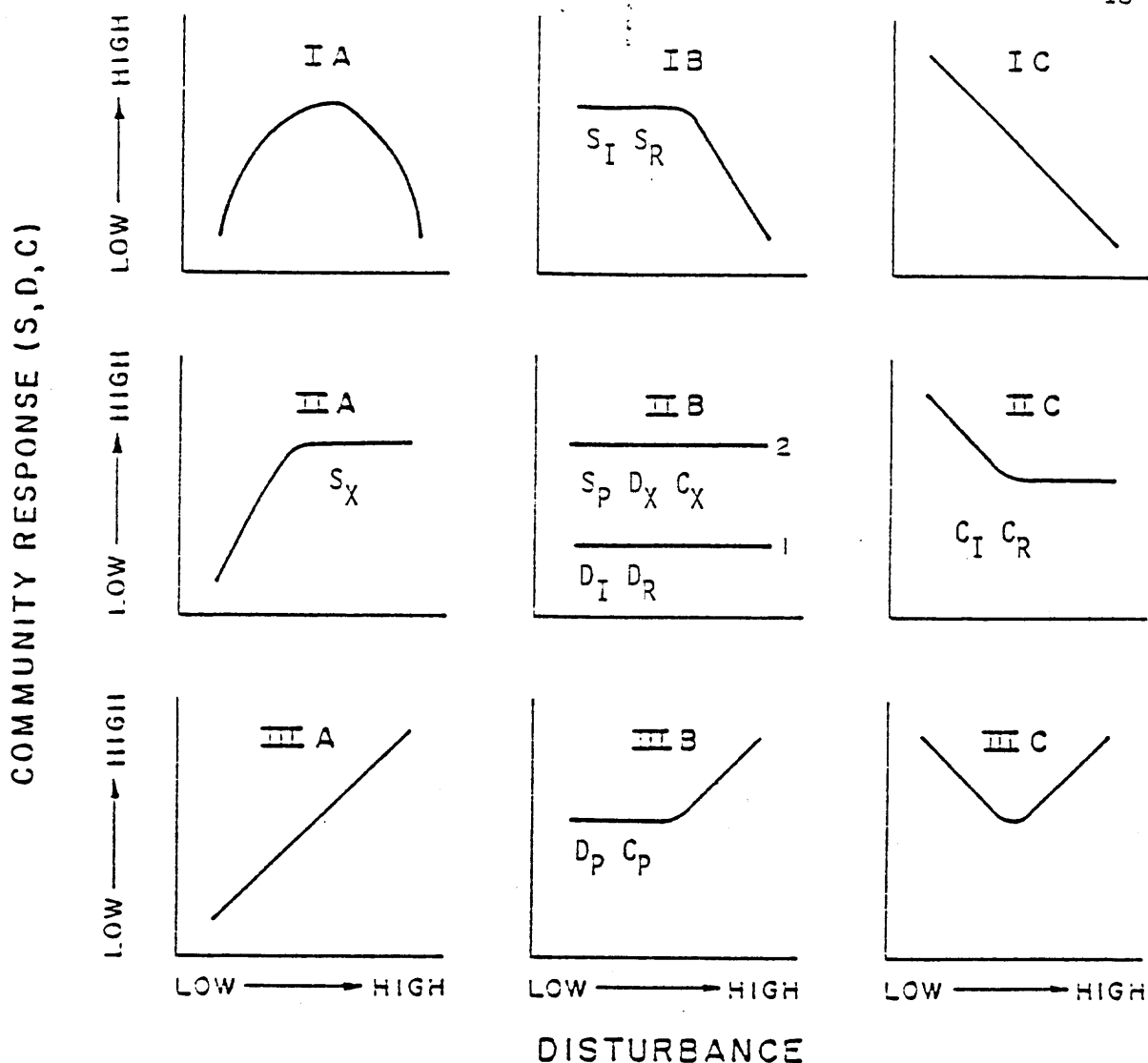
DISTURBANCE

Figure 2.2:   The nine possible community response curves for species richness (S), density (D) and cover (C) to disturbance in the presence of other environmental gradients, such as competition or moisture availability.   The effects of disturbance are strong in Type I curves, moderate in Type II curves and weak in Type III curves.   The effects of gradients that are negatively correlated with disturbance (e.g. moisture stress, competition, etc.) are strong in Type A curves, moderate in Type B curves and weak in Type C curves.   Horizontal or greater than horizontal segments of curves are attributed to weak gradient responses or adaptation by constituent species to the gradients.   Subscripts indicate riparian plant community responses described in the text for intermittent (I), perennial (P), Colorado River (R) and springs (X). Gradient effects positively correlated with disturbance were not considered.

gradients less than 15° were selected for censusing, eliminating another 33 canyons (25.2% of the total) from consideration. Three 2 x 3m plots were randomly located in each tributary 25m above the 800m^3/sec stage of the Colorado River, an elevation above potential effects of the 1884 flood-of-record for the Colorado River (8,500m^3/sec; R. Webb personal communication). One plot was located on the stream channel terrace (Zone 1 = high disturbance, annually flooded), a second plot above the first overbank terrace (Zone 2 = intermediate disturbance, with flooding approximately every 3 to 20 years), and the third plot was located on the debris flow terrace (Zone 3 = low disturbance with a flood interval of > 20 to 200 years; Figure 2.3). I defined "riparian vegetation" as any perennial plant life occurring in the flood zone of a channel, including phreatophytes which have direct contact with the water table, and xerophytes from the surrounding desert whose populations are maintained by repeated colonization (Reichenbacher 1984; Shmida and Milson 1985). All perennial plants on plots were identified (S), counted (D), and basal area was measured (C). The taxonomy of Phillips et al. (1987) was followed. Acacia greggii was included as a strongly facultative riparian species. Substrate texture, presence of ground cover or duff, and shrub cover were evaluated at 15 points in each plot, and elevation, exposure, channel and canyon width, stream type (perennial = wet, intermittant or ephemeral = dry), basin area and stream depth were measured at each site. Preliminary analyses of species - area relationships suggested that 2 x 3m plots provided a representative sample of species and maximized sampling efficiency. Adequacy of the 2 x 3m plot size was evaluated by generating species accumulation curves from eighty 2 x 100m transects in the system.

The figure shows a cross section with labels: ZONE 3, ZONE 2, ZONE 1, CLIFF, TALUS, LOW DISTURBANCE, INTERMEDIATE DISTURBANCE, HIGH DISTURBANCE, TRIBUTARY CHANNEL.
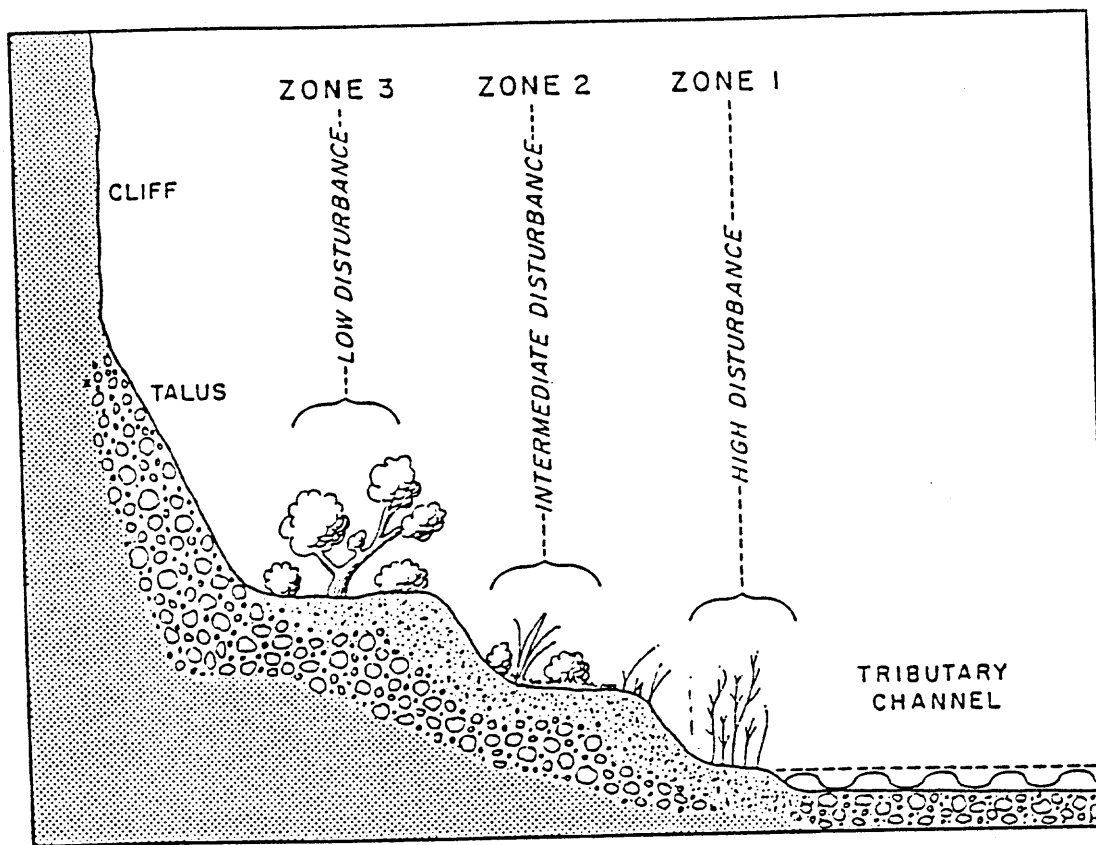
Figure 2.3: An idealized cross section of a stream channel showing the three flood zones censused. Zone 1 lay along the annually flooded channel margin; Zone 2 lay in the intermediate disturbance zone above the first overbank terrace, which was flooded on a 3 to 20 yr cycle; and Zone 3 occupied the 20-200 yr recurrent flood terrace caused by debris flows.

Comparably collected 2 x 3m plot data were used to compare the riparian vegetation of the dam-controlled Colorado River corridor with that of the unregulated tributaries. The same physical and vegetation data (above) were collected on 50 randomly selected 2 x 3m plots throughout the river corridor in each of 3 flood zones, including: 1) the $800m^3$/sec terrace (Zone 1), which was flooded annually, on average, during the post-dam era from 1963 to 1988; 2) the $1,700m^3$/sec terrace (Zone 2), which was flooded twice during the 25-year post-dam era (1965 and 1983); and 3) the $3,550m^3$/sec terrace (Zone 3) which was flooded on an 11 to ca. 100 year cycle during the pre-dam era, with the most recent flooding in 1921 (Howard and Dolan 1980). Thus the flood zones selected in the river corridor corresponded closely to those examined in the tributaries; however, because all data were gathered from one stream system (the Colorado River), analyses were conducted independently of the tributary data, and only gross comparisons with tributary vegetation patterns were made.

Variation in disturbance levels under uniformly high moisture availability was examined in large springs that mouthed into otherwise dry tributary channels and thereby created perennial streams. Three springs with southerly exposure were selected in the Grand Canyon at an absolute elevation between 500m and 900m and having a relative elevation of more than 25m above the $800m^3$/sec Colorado River stage: Nankoweap Spring (RK 84.5), Deer Creek Spring (RK 220) and Spring Canyon Spring (RK 328). Three randomly selected 2 x 3m plots were censused in each of the three disturbance zones at each spring site.

S, logeD and logeC were response variables used in MANOVA analyses of tributary type (intermittent versus perennial), Zone (1 to 3),

substrate (fine, gravel/broken rock, bedrock), and cardinal exposure (N, S, E or W) of the reach as independent factors; $\log_e$ elevation as a covariate; with tributaries as replicates, with $\log_e$ transformation used to achieve homoscedasticity of variance between treatments. Wilk's lambda approximate F (F_W), a commonly used likelihood ratio, was employed as a test statistic (Johnson and Wichern 1982). To determine the relevance of IDH predictions, S was evaluated separately for ephemeral and perennial tributaries using the nonparametric Quade Test and Quade range test (Conover 1980: 294-297), with three disturbance levels (low, medium and high frequency flood terraces) within blocks (tributaries). The Kruskal-Wallis test (Conover 1980: 229-231) was similarly employed for analysis of S from river corridor sites.

To evaluate trends in community composition and similarity, importance values were calculated and compared for each plant species which comprised more than 1% of the total abundance or cover in each stream type and flood zone (Brower and Zar 1984). Shannon-Weiner H' (Pielou 1966) was calculated for pooled data for each stream type (dry or wet tributaries, and Colorado River sites) in each zone (low, medium and high disturbance terraces), and all possible pairwise combinations of H' in these 9 (stream type x zone) settings were compared.

Results

Geomorphology

Flood frequency appeared well correlated with patterns of terrace formation and tributary channel geomorphology. Flood disturbance frequency in the three flood zones was consistent with the conclusions of Hereford (1984) and Webb et al. (1987) who examined channel morphology and debris flows in this system. All but one tributary

showed evidence of recent (< 1yr) flood scouring or jetsam in Zone 1, and virtually all Zone 2 plots contained driftwood or other evidence of flooding judged to have been deposited within the past decade, but none within the past year. Zone 3 plots revealed little flood-deposited driftwood or other jetsam of recent age, attesting to the relative infrequency of flood disturbance of upper terraces.

Intermittent and Perennial Tributary Vegetation

Tributary vegetation composition differed significantly between intermittent and perennial stream types. All zones in intermittent streams were strongly dominated by xerophytes (e.g. Ephedra spp., Encelia farinosa and various Cactaceae (Figure 2.4). Perennial stream sites were strongly dominated by shallow-rooted, clonal riparian phreatophytes which required fine particle substrates and abundant soil moisture, such as Juncus spp., Equisetum spp., Salix exigua, Alhagi camelorum, Mimulus cardinalis and Tessaria sericea) on high and intermediate disturbance terraces (Gary 1963). Low disturbance zones in perennial tributaries were dominated by deeply-rooted Prosopis glandulosa and Acacia greggii. Partial correlation coefficients between S with D and C were 0.491 and 0.386, respectively, demonstrating that primary vegetation characteristics were somewhat intercorrelated and not independent.

Community parameters responded significantly to several major treatment factors, including flood zone, stream type, substrate texture and cardinal exposure, and $\log_e$ elevation as a covariate (Table 2.1). Overall, the pooled tributary species list revealed significantly fewer species (56 species) in Zone 1, and equivalent total S in zones 2 and 3 (69 and 70 species, respectively; $Chi^2 = 1.877$, df = 2, $p < 0.05$). S, D
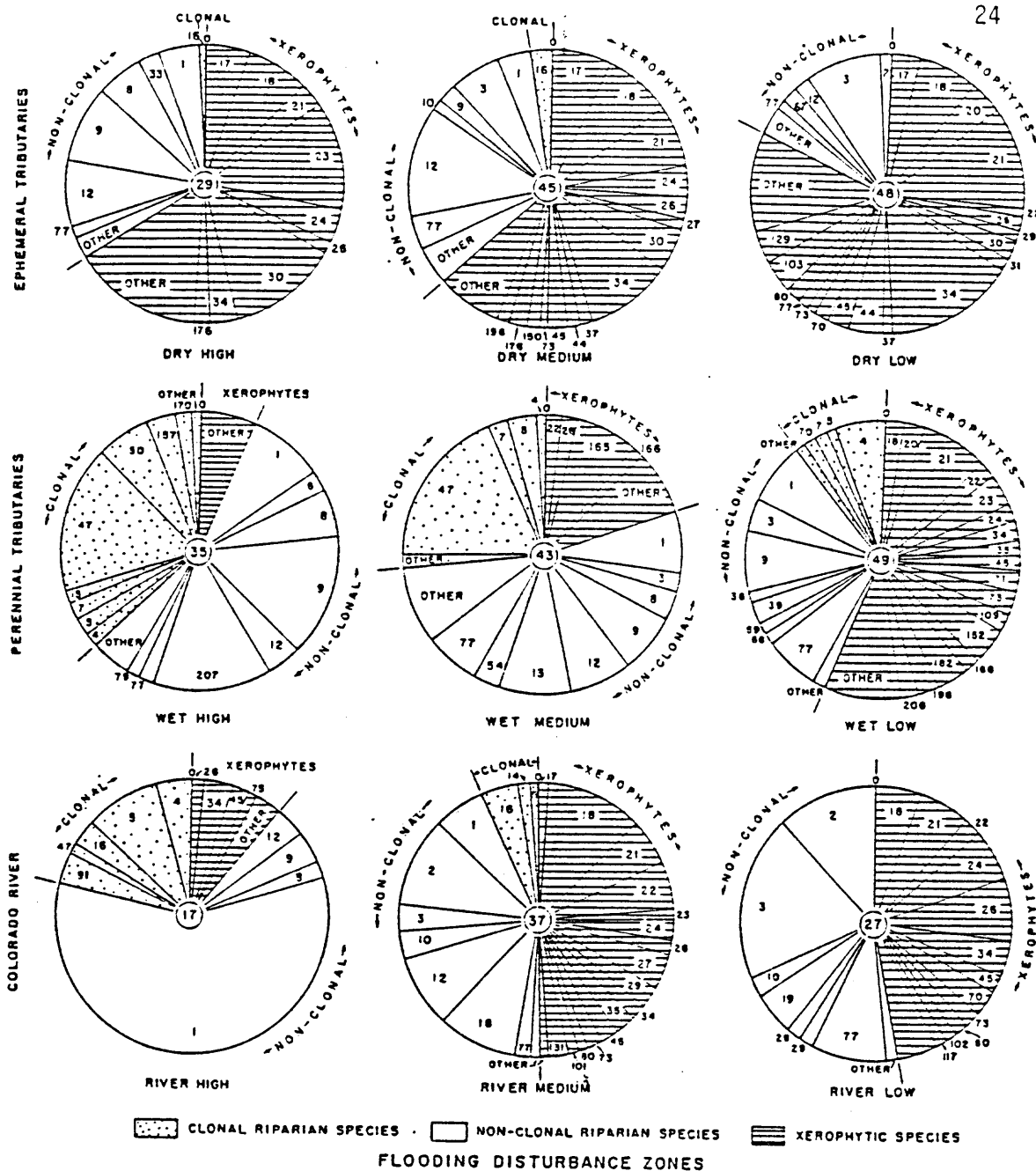
Figure 2.4: Relative importance values for all species comprising 1 percent or more of the total summed community importance value. Data are pooled by flood zone in intermittent (dry), wet (perennial) and Colorado River stream types. Central numbers show the pooled species richness in each zone and stream type.

Table 2.1: Intermittent and perennial tributary riparian vegetation characteristics in Grand Canyon, Arizona. A 4-factor MANOVA analysis using: species richness (S), $\log_e$ stem density (no./m^2, D) and $\log_e$ cover (basal area in $cm^2 \cdot m^{-2}$, C) as response variables; flood disturbance (3 zones), tributary type (intermittent or perennial), cardinal exposure (4 compass directions) and $\log_{10}$ mean substrate particle diameter (texture) as predictors; $\log_e$ drainage basin area and $\log_e$ elevation(m) as covariates; and with 59 replicates of intermittent tributaries and 26 replicates of perennial tributaries.

RESPONSE SOURCE VARIABLES	WILK'S LAMBDA APPROXIMATE F	DF	SIGNIF. OF P	SIGNIF. OF
MAIN EFFECTS				
Constant	2.949	3, 194.0	0.034	A^{**}
Exposure (E)	2.154	9, 472.3	0.024	S^*
Substrate Texture (T)	3.425	6, 388.0	0.003	D^{**}, C^{***}
Stream Type (Dry vs. Wet) (Str)	31.926	3, 194.0	0.000	S^{***}, D^{**}, C^{***}
Flood Zone (Z)	16.757	6, 388.0	0.000	S^{***}, D^*, C^{***}
INTERACTION EFFECTS:				
E by T	1.610	18, 549.2	0.053	---
E by Str	1.122	9, 472.3	0.345	---
E by Z	1.441	18, 549.2	0.107	---
T by Str	3.336	6, 388.0	0.003	D^{***}
T by Z	1.611	12, 513.6	0.085	---
Str by Z	4.605	6, 388.0	0.000	S^*, D^{***}
E by T by Str	1.490	12, 513.6	0.124	---
E by T by Z	1.508	24, 563.3	0.058	---
E by Str by Z	1.388	18, 549.2	0.131	---
T by Str by Z	1.116	9, 472.3	0.349	---
E by T by Str by Z	1.063	9, 472.3	0.389	---
COVARIATE EFFECTS:				
Regression	2.308	6, 388.0	0.034	D^*

D: Elevation (t_{regr} = 2.830, p = 0.005, df = 2,196) (a negative correlation)

* p < 0.05; ** p < 0.01; *** p < 0.001

and C were significantly greater in perennial tributary plots than in intermittent tributaries (figures 2.5, 2.6, 2.7). D and C were significantly greater in zones 2 and 3 (especially in perennial tributaries) than in Zone 1 (especially in intermittent tributaries). S was significantly (25%) higher in settings with southerly exposure as compared to other cardinal exposures. D and C were significantly higher in fine (silt and/or sand) substrates, as compared to cobble or bedrock substrates. Significant interaction effects for D occurred between stream type and substrate type because the pattern of decreasing D across the substrate gradient (increasing particle size) was reversed in intermittent versus perennial tributaries: thus, silt/sand substrates supported high D in perennial tributaries but low D in intermittent tributaries. Significant interaction effects occurred for S and D between terraces and stream types: S was significantly lower in Zone 1 in intermittent tributaries, but not in perennial tributaries; and D was significantly higher in zones 2 and 3 in perennial tributaries, but equivalent in intermittent tributaries. A significant positive correlation existed between D and elevation (analyzed as a covariate).

Analysis of species-area relationships showed that the 2 x 3m plot size sampled, on average, 28.7% of the total available number of species in any plot (R^2_{adj} = 52.8%, p < 0.001, df = 1,416). The large sample size provided sufficient power to justify this plot size.

Even without consideration of other vegetation characteristics, univariate nonparametric analyses indicated that S failed to match the predictions of the IDH (Figure 2.5). Although S varied significantly between flood zones in intermittent tributaries (Quade t = 14.163, p < 0.01, df = 2,58), S was statistically equivalent in zones 2 and 3,
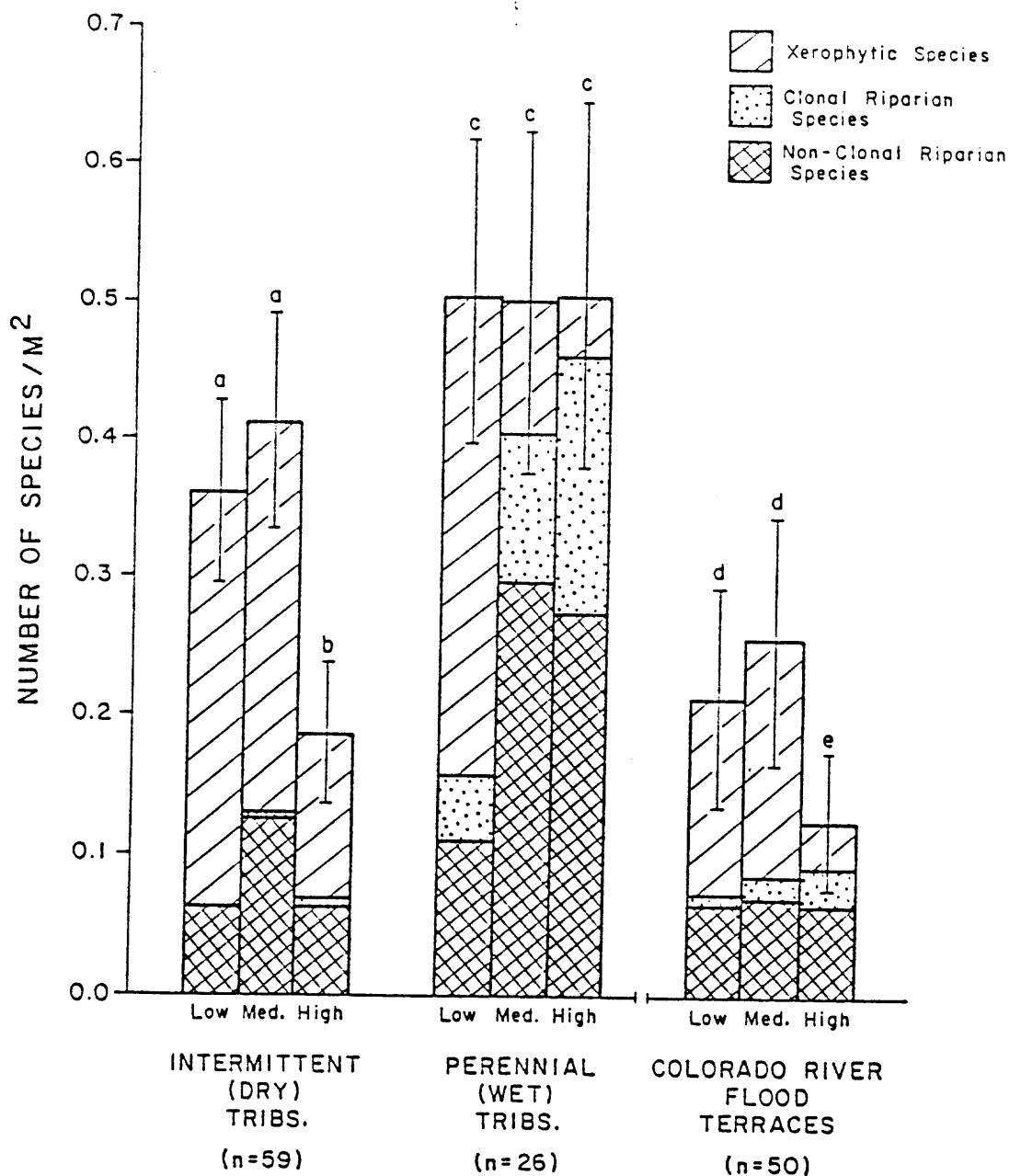
Figure 2.5:   Mean number of species/m^2 of perennial plants in intermittent (dry) and perennial (wet) tributaries, and along the Colorado River in Grand Canyon, on low, intermediate and high disturbance flood terraces.   Lower case letters signify univariate, within-stream-type Student-Neuman-Keuls range test results.   Tributary data were analyzed separately from Colorado River data.   Bars indicate 95% confidence intervals.
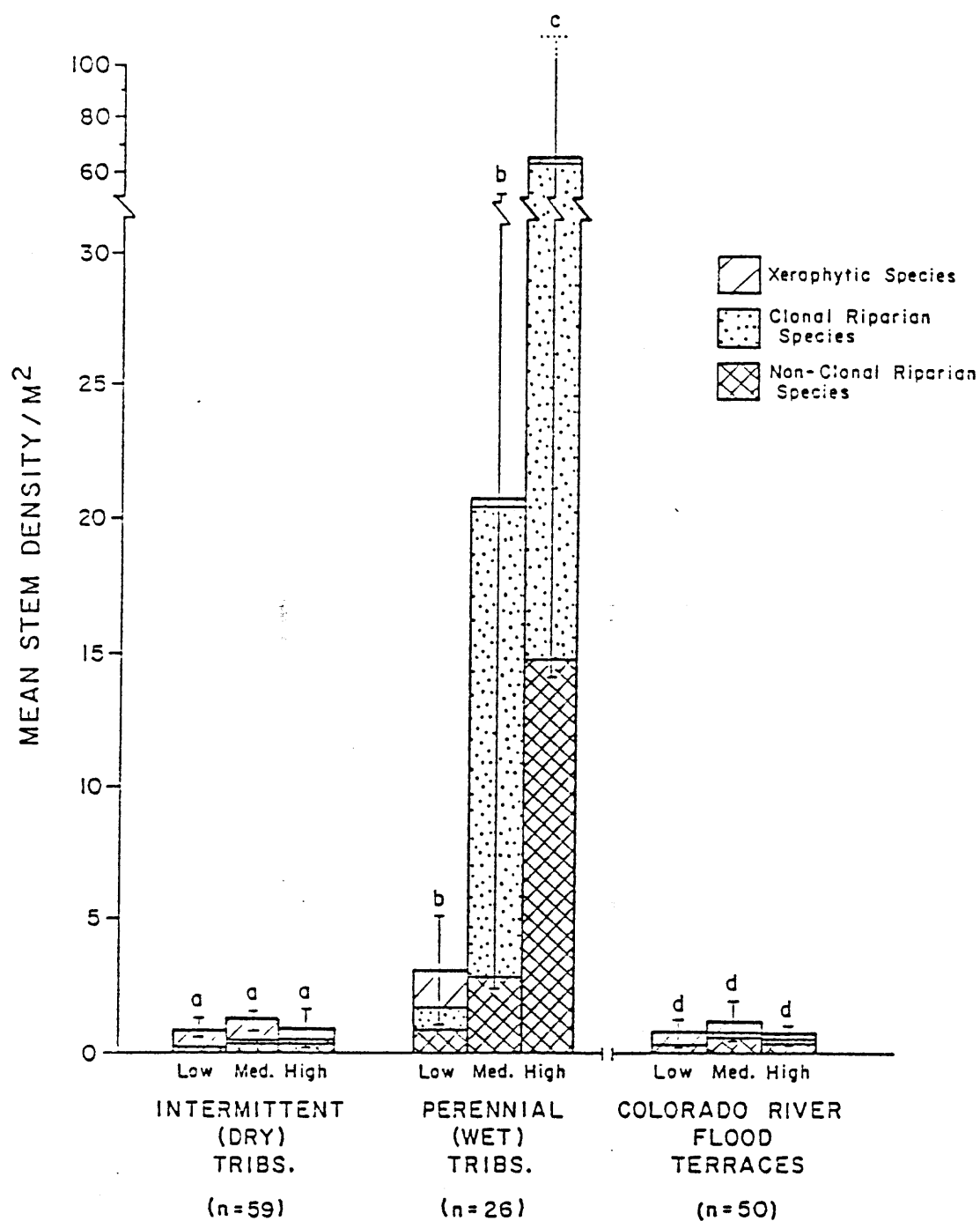
Figure 2.6: Mean stem density (D = number of stems/m^2) of perennial plants in intermittent (dry) and perennial (wet) tributaries, and along the Colorado River in Grand Canyon, in low, intermediate and high flood disturbance zones. Lower case letters signify univariate, within-stream-type Student-Neuman-Keuls range test results. Tributary data were analyzed separately from Colorado River data. Bars indicate 95% confidence intervals.
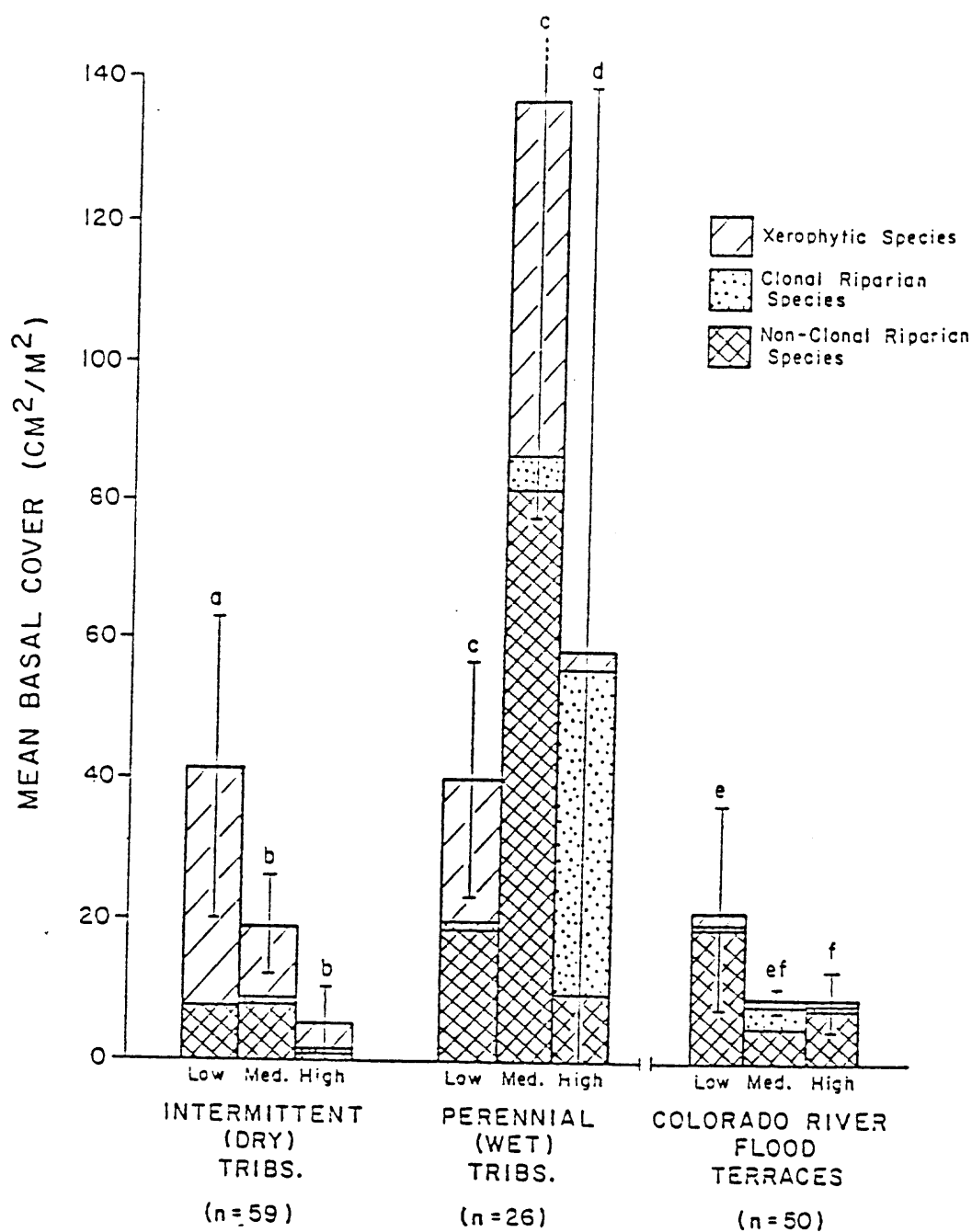
Figure 2.7: Cover (C = mean basal area in cm2/m2) of perennial plants in intermittent (dry) and perennial (wet) tributaries, and along the Colorado River, in low, intermediate and high flood disturbance zones. Lower case letters signify univariate, within-stream-type Student-Neuman-Keuls range test results. Tributary data were analyzed separately from Colorado River data. Bars indicate 95% confidence intervals.

resembling the community response pattern depicted in Figure 2.IB. was uniformly high and equivalent across the disturbance gradient in perennial tributaries (t_{Quade} = 0.0003, p > 0.25, df = 2,29).

In summary, disturbance effects were significant in intermittent tributaries but not in perennial tributaries, while S did not respond to low versus intermediate disturbance levels. Therefore the expected gradient interactions were not manifest under low disturbance conditions. The predictions of the IDH were not met by the following MANOVA results for riparian vegetation: 1) a slight trend of maximal S (log-transformed or not) on intermediate disturbance terraces along intermittent streams was swamped by extreme variance, and was not evident at all in perennial stream sites (Figure 2.5); 2) a trend in D showing the IDH curve was swamped by variance in intermittent streams and D was strongly, positively correlated with disturbance in perennial streams (Figure 2.6); and 3) C was negatively correlated with disturbance in intermittent tributaries (Figure 2.7). In addition, the pooled species list for all tributaries showed that S was negatively correlated with disturbance but did not differ in zones 2 and 3.

The plant communities occupying different terraces and different stream types responded to disturbance but were compositionally dissimilar. This was demonstrated by the following results: 1) H' and J' were negatively correlated with disturbance; 2) H' and J' were higher in intermittent than in perennial tributaries or river corridor sites; 3) H' was generally significantly different between zones 1 and 2, but not significantly different among Zone 3 in all three stream types (Table 2.2). Supporting this latter result, regression of species' relative importance values between terraces and sites revealed that

Table 2.2: Comparison of H' diversity within and between stream types. H' values were generated from perennial plant associations on low (L), intermediate (M) and high (H) disturbance flood terraces in intermittent (I, n = 59), perennial (P, n = 26) and Colorado River corridor (R, n = 50) sites. Values are t, p (df), statistics were derived from Hutcheson (1970).

	I-L	I-M	I-H	P-L	P-M	P-H	R-L	R-M	R-H
I-L	0.000 nsd (118)	0.942 nsd (118)	11.158 *** (113)	1.707 nsd (34)	9.744 *** (37)	11.776 *** (39)	6.294 *** (110)	3.944 *** (109)	14.369 *** (107)
I-M	0.942 nsd (118)	0.000 nsd (119)	10.224 *** (115)	1.213 nsd (34)	9.213 *** (37)	11.225 *** (38)	5.388 *** (110)	3.040 ** (109)	13.445 *** (109)
I-H	11.158 *** (113)	10.224 *** (115)	0.000 nsd (122)	3.752 *** (31)	3.861 *** (33)	5.662 *** (34)	4.907 *** (104)	6.701 *** (100)	3.315 ** (117)
P-L	1.707 nsd (34)	1.213 nsd (34)	3.752 *** (31)	0.000 nsd (52)	5.677 *** (51)	73.222 *** (50)	1.589 nsd (34)	0.404 nsd (35)	5.175 *** (30)
P-M	9.744 *** (37)	9.213 *** (37)	3.861 *** (33)	5.677 *** (51)	0.000 nsd (52)	1.168 nsd (51)	6.094 *** (36)	7.356 *** (37)	2.313 * (32)
P-H	11.776 *** (39)	11.225 *** (38)	5.662 *** (34)	73.222 *** (50)	1.168 nsd (51)	0.000 nsd (52)	7.951 *** (38)	9.258 *** 39)	4.045 *** 33)
R-L	6.294 *** (110)	5.388 *** (110)	4.907 *** (104)	1.589 nsd (34)	6.094 *** (36)	7.951 *** (38)	0.000 nsd (102)	2.234 * (101)	7.499 *** (98)
R-M	3.944 *** (109)	3.040 ** (109)	6.701 *** (100)	0.404 nsd (35)	7.356 *** (37)	9.258 *** (39)	2.234 * (101)	0.000 nsd (101)	9.750 *** (94)
R-H	14.369 *** (107)	13.445 *** (109)	3.315 ** (117)	5.175 *** (30)	2.313 * (32)	4.045 *** (33)	7.499 *** (98)	9.750 *** (94)	0.000 nsd (100)
H'	1.365	1.326	0.943	1.230	0.681	0.579	1.106	1.198	0.836
J'	0.812	0.802	0.645	0.728	0.417	0.375	0.773	0.796	0.679

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; nsd $p > 0.05$

communities on adjacent zones within a stream type were most similar. For example, relative importance values for each plant species in Zone 1 in perennial tributaries were most highly correlated with those of Zone 2 in perennial tributaries, and correlation decreased in Zone 3 and between other stream types (Table 2.3).

Spring Source Vegetation

(Spring source) were used to examine disturbance effects under constant, high moisture availability. The springs were uniform in most characteristics such as water volume and southerly exposure; however, the headwaters of two of the three springs welled up from the ground, and the sources were completely dominated by Phragmites australis and Cladium californicum. The third spring, Deer Creek Spring, plunged from a cliff face, had a several ha. drainage and steep, eroding banks, suggesting that its channel was not stable. Spring data showed that the distribution of S followed the Type IIA curve (Figure 2.2), increasing at intermediate and high disturbance (F_W = 3.469, p = 0.010, df = 6,30.0; Figure 2.8). Significant interaction effects between site and terrace with p_S = 0.004, df = 2,17). Trends towards the IDH curve were swamped by variance for D and C, resulting in Type IIB curves were attributed to the individual spring differences: S was uncorrelated with disturbance at Deer Creek Spring; D was positively correlated with disturbance at Nankoweap Spring, and C varied widely at all 3 springs.

Colorado River Vegetation

The vegetation of the Colorado River corridor was structurally similar to that of intermittent tributaries (figures 2.5, 2.6, 2.7), with low overall plant density, but more clonal and fewer xerophytic

Table 2.3: Riparian plant community similarity within and between stream types. Matrix of coefficient of determination (r^2) and significance of regression F for correlation between the importance value of each riparian plant species in each low (L), intermediate (M) or high (H) disturbance flood terraces in intermittent (I), perennial (P) or Colorado River (R) stream types with each other terrace and setting (df = 1,116).

	I-L	I-M	I-H	P-L	P-M	P-II	R-L	R-M	R-H
I-L	1.000 ***	0.478 ***	0.067 **	0.114 ***	0.001 nsd	0.012 nsd	0.273 ***	0.124 ***	0.000 nsd
I-M	0.478 ***	1.000 ***	0.333 ***	0.141 ***	0.036 nsd	0.005 nsd	0.166 ***	0.304 ***	0.035 nsd
I-H	0.067 **	0.333 ***	1.000 ***	0.112 ***	0.033 nsd	0.049 nsd	0.023 nsd	0.116 ***	0.034 nsd
P-L	0.114 ***	0.141 ***	0.112 ***	1.000 ***	0.071 **	0.074 **	0.089 **	0.057 *	0.157 ***
P-M	0.001 nsd	0.036 nsd	0.033 nsd	0.071 **	1.000 ***	0.440 ***	0.007 nsd	0.016 nsd	0.085 **
P-H	0.012 nsd	0.005 nsd	0.049 nsd	0.074 **	0.440 ***	1.000 ***	0.005 nsd	0.001 nsd	0.083 **
R-L	0.273 ***	0.166 ***	0.023 nsd	0.089 **	0.007 nsd	0.005 nsd	1.000 ***	0.228 ***	0.000 nsd
R-M	0.124 ***	0.304 ***	0.116 ***	0.057 *	0.016 nsd	0.001 nsd	0.228 ***	1.000 ***	0.072 **
R-H	0.000 nsd	0.035 nsd	0.034 nsd	0.157 ***	0.085 **	0.083 **	0.000 nsd	0.072 **	1.000 ***

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; nsd $p > 0.05$
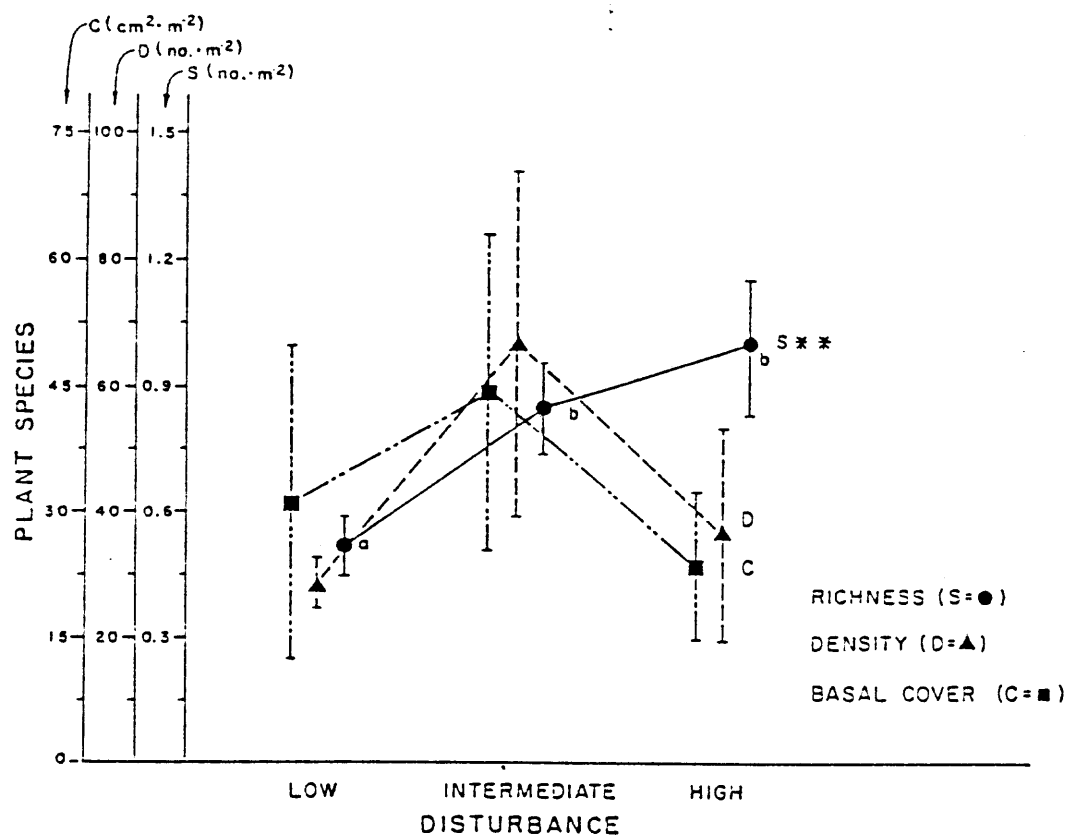
Figure 2.8: Species richness (S as number of species/m2), mean stem density (D as number/m2) and basal area (C as cm2/m2) of perennial plants on low, intermediate and high disturbance flood terraces at three south-facing springs in the Grand Canyon, Arizona. Three 2 x 3m plots were sampled in each zone at each spring. ** indicates p < 0.01.

species, and dominance by _Tamarix ramosissima_ in Zone 1 (Figure 2.4). Mean and confidence intervals for S in the river corridor generally overlapped with those of intermittent, but not perennial tributaries, and patterns of S most closely resembled that depicted by the Type IB curve (Figure 2.2). MANOVA analyses revealed significant effects of substrate texture on S and D, and flood zone on C, but no effect of cardinal exposure (Table 2.4). A significant interaction effect for C between substrate and exposure occurred because C was positively correlated with particle size on north- and south-facing sites, but was negatively correlated or interacted in a complex fashion on west- and east-facing sites. Cover of _Prosopis_, _Acacia_ and xerophytes, especially Cactaceae was greater on low disturbance terraces, while clonal and non-clonal riparian species dominated channel margins and intermediate disturbance terraces, respectively. S did not vary significantly between zones, as shown by univariate the Kruskal-Wallis test (W = 4.321, p > 0.10, df = 2). In comparison with dry tributaries, river sites contained lower S and comparable D across all zones, and lower C in low and intermediate zones, but higher C in Zone 1. River sites were lower in all community characteristics as compared to perennial tributaries, although differences between wet and river sites decreased in Zone 3.

Table 2.4: Colorado River riparian vegetation characteristics in Grand Canyon, Arizona. A 3-factor MANOVA analysis using: species richness (S), $\log_e$ stem density/m^2 (D) and $\log_e$(basal area) in $cm^2 \cdot m^{-2}$ (C) as response variables; flood zone (3 terraces), cardinal exposure (4 compass directions) and substrate texture (3 classes) as response variables; and $\log_e$ elevation(m) as a covariate, with 50 replicates of each flood zone.

RESPONSE SOURCE	WILK'S LAMBDA APPROXIMATE F	DF	SIGNIF. OF F	SIGNIF. OF VARIABLE(S)
MAIN EFFECTS:				
Constant	0.523	3, 109.0	0.667	---
Exposure (E)	1.091	9, 265.3	0.370	---
Substrate Texture (T)	4.764	6, 218.0	0.000	S^{**}, D^*
Flood Zone (Z)	2.268	6, 218.0	0.038	C^*
INTERACTION EFFECTS:				
E by T	1.768	18, 308.8	0.028	C^*
E by Z	0.582	18, 308.8	0.912	---
T by Z	1.281	12, 288.7	0.229	---
E by T by Z	0.889	33, 321.8	0.647	---
COVARIATE:				
Regression:	0.098	3, 109.0	0.961	---

* $p < 0.05$; ** $p < 0.01$

Discussion

Plant community structure is regulated by spatially and temporally variable environmental gradients whose axes and intersections define a selection regime in which fitness is tested (Watt 1947; Whittaker 1967; Grime 1977; Whittaker and Levin 1977; White 1979; Sousa 1984; Schmida and Milson 1985; Tilman 1885, 1988). The results presented here demonstrated that the riparian plant community in the Grand Canyon was structured by interaction between moisture availability, disturbance, exposure, and adaptation of constituent species to those gradients. Competition was not implicated as a community structuring mechanism, except at spring sources. Riparian vegetation along the Colorado River resembled that in intermittent tributaries, not perennial tributaries. These results supported the gradient interactions/ adaptation hypothesis, not the intermediate disturbance hypothesis (IDH).

Flood disturbance effects on community structure were conditionally dependent on moisture availability. Disturbance exerted a significant negative impact on plant species richness (S), density (D) and basal area (C) in high disturbance zones in the dry tributary canyons that typify Grand Canyon drainages; however, S was equivalent and C decreased between low and intermediate disturbance zones. In perennial tributaries, high disturbance zones (with high moisture availability) supported a profuse, diverse association of flood-adapted, predominantly clonal phreatophytes, such as Equisetum, Juncus, Typha, Tessaria, Phragmites and Salix exigua, while low and intermediate flood zones supported an equivalent S consisting of different species in far lower densities. S was positively correlated with disturbance at spring sources which were stable and had high moisture availability.

Gradients and factors other than disturbance and moisture availability influenced riparian plant community structure. Significantly higher S on south-facing sites seemingly contradicted the hypothesis of moisture availability as a limiting resource. South-facing slopes have hotter, drier microclimates in the Southwest, and this moisture stress might be expected to decrease, not increase, S. This deep-canyon, desert riparian system is subject to cold winter weather, and many xerophytic species in the system reach their northernmost range limit on the floor of the Grand Canyon. Subsidence of cold air down tributaries and shading from the 1,500m high rims during the winter months undoubtedly places Cactaceae, Encelia, Fouquieria, Larrea and other poorly cold-adapted and shade-adapted xerophytes at a considerable selective disadvantage. Shading effects on xerophytes should be most severe on north-facing slopes and least on south-facing slopes, and cold-flow effects should be most pronounced on the channel floor (e.g. on high-disturbance terraces). Therefore the phenomenon of increased S on south-facing sites was attributable to improved thermal conditions, and perhaps light availability, for xerophytes during winter months, and suggested that thermal and light regimes were important abiotic gradients in this system. Substrate texture also played a structuring role in community composition. Stress associated with gradients of nutrient availability (Scala 1984; Stevens and Waring 1988) and herbivory (Stevens 1985) lie parallel to, and appear positively correlated with the moisture stress gradient in this system; however, these other gradients appear to be epiphenomenal in comparison with the moisture stress gradient in the Grand Canyon.

Differences in constituent species' degree of adaptation to environmental gradients played a critical role in community structure in this system. Individual species abundance and cover changed markedly from terrace to terrace within and between stream types. For example, dominant species in Zone 1 varied tremendously between stream types: several xerophytic species dominated Zone 1 in intermittent streams; _Equisetum_ often dominated Zone 1 in perennial tributaries; and _Tamarix_ dominated Zone 1 along the Colorado River. None of these species was dominant on other terraces within or between the three stream types. Community structure and composition varied least in low disturbance zones in between-stream-types and between-flood-terrace comparisons.

The conflicting selective demands of moisture stress and flood stress on riparian plant species have apparently been of sufficient strength to prevent adaptation of native plant species to the rigors of the highly disturbed channel margins in intermittent tributaries. This was illustrated by low community similarity between the plant associations along the channel margins in dry and wet drainages. _Brickellia longifolia_ was the most ubiquitous species in high disturbance intermittent tributary environments, and was a low-growing, resinous species which was both moderately flood tolerant and drought tolerant. The high disturbance zones in dry tributaries were virtually devoid of the clonal riparian species (e.g. _Salix exigua_, _Aster spinosus_, _Tessaria sericeae_, and several macrophytic monocot species) that typified channel margins in perennial tributaries. _Tamarix_ appeared more eurytolerant of moisture and flood stress than did native species, in part accounting for its abundance in the high disturbance zone along the Colorado River (Stevens and Waring 1985, 1988).

Competition did not regulate species richness, except in undisturbed spring sources with high moisture availability. Moisture gradient effects masked or overrode competition effects in most riparian sites, as demonstrated by: 1) a Type IB curve for S, a Type IIB.1 curve for D, and a Type IIC curve for C in intermittent tributaries; 2) significantly lower D and C in all flood zones in intermittent, as compared to perennial tributaries; 3) dominance of xerophytes (e.g. Encelia, Ephedra and Opuntia) as compared to riparian phreatophytes (e.g. Salix, Baccharis and Tamarix), especially in Zone 1 in intermittent tributaries; and 4) greater community similarity between Zone 2 and Zone 3 in each stream type (Figure 2.2). Elsewhere (Chapter 3) I presented data showing no evidence of direct competition between two dominant perennials in this system. The only riparian setting in which competition was implicated in community organization was in undisturbed spring sources where clonal, macrophytic monocots (especially Phragmites and Cladium) dominated or were the sole occupants. Thus spring sources provided conditions which favored clonal growth strategies and where competition reduced S. These findings support the conclusions of Fowler (1986: 98) and Grimes and Hodgson (1987) that competition was strongest in productive, undisturbed sites.

River regulation is an unusual form of man-caused disruption because it alters the riparian environment by mollifying, rather than intensifying, a significant natural disturbance regime (Stanford and Ward 1979; Howard and Dolan 1980; Turner and Karpiscak 1980). In comparison with tributaries, the Colorado River corridor vegetation appeared structurally and compositionally similar to that of intermittent tributaries, although more depauperate and more dominated

by clonal phreatophytes in the high disturbance zone. These results suggested that despite impoundment and discharge regulation: 1) river corridor vegetation structure was strongly influenced by moisture availability; 2) there was little evidence of competition, particularly with the Type IIC curve noted for C; and 3) after 25 years of regulated discharge, river corridor vegetation is still in the early stages of development, as evidenced by low S and C in Zone 1 and as compared to perennial tributary vegetation. Low moisture availability was held responsible for failure of Prosopis recruitment in Zone 3, and a general absence of vegetation in Zone 2 (Carothers et al. 1979; Anderson and Ruffner 1988; Pucharelli 1988; Waring and Stevens 1988). Historical changes in discharge left a pre-dam community of Prosopis and Acacia perched above the 3,550m^3/sec stage in this system, increased S, A and C above what present conditions permit, and obscured the interaction effects of disturbance and moisture stress. As these perched, pre-dam phreatophyte stands senesce and disappear, the river vegetation profile should more strongly reflect the strength of the moisture gradient.

These results supported the predictions and mechanisms of the "gradients/adaptation hypothesis", not the IDH, and no IDH patterns were found for any response variable in any stream type. The IDH was not supported because competition was not demonstrated to influence diversity in low disturbance zones, except in rare spring source settings with high moisture availability and low disturbance. Tributary community responses were generally equivalent or higher in low disturbance zones as compared to intermediate disturbance zones, or slight differences were swamped by variance. Discharge regulation in the Colorado River corridor should have released diversity in Zone 1,

and should have produced Type IIA or IIIA curves for S. Instead, uncorrelated (D, Type IIB.1 curve) or negative (S, Type IB curve; C, Type IIC curve) correlations were observed for all community characteristics (Figure 2.2). The predictions of the IDH may obtain for riparian vegetation in environments where increased moisture availability on low disturbance terraces permits stronger competition, for example: 1) at higher, but not boreal, elevations, 2) in more mesic environments, or 3) during pluvial periods in the past.

Gradients effects vary spatially and temporally between ecosystems. In this system, flood-related disturbance impacts on riparian vegetation were conditionally modified by moisture availability, and competition played a minor role in community structure. (Nomothetic models) of community organization must be based on those critical gradients actually affecting a system, not on gradients presumed important from a priori assumptions, and these models must not ignore the contributions to community structure made by differential adaptation to gradients.

CHAPTER 3:

AGE-SPECIFIC COMPETITION BETWEEN
EXOTIC TAMARISK AND NATIVE COYOTE WILLOW IN THE GRAND CANYON

Introduction

Despite an embarassment of literature on the role of interspecific competition in plant community succession, thorough and ecologically relevant investigations of the kinds and intensity of competition between perennial plant species remain rare (Watt 1947; Connell and Slayter 1977; Harper 1977; Grubb 1977; Grime 1979; Grime and Hodgson 1987; Huston and Smith 1987; Menge and Sutherland 1987). This lack of data may be attributed to several problems: 1) competitive interactions range from indirect, density-dependent resource exploitation to direct, density independent inhibition of recruitment and/or growth (Schoener 1983; Grime and Hodgson 1987); 2) competitive ability varies throughout an individual's lifetime, rendering studies of long-lived perennial plants difficult (Grubb 1977; Harper 1977); and 3) data and experimental designs testing competition are much disputed, and are difficult to analyze and interpret (e.g., de Wit 1960; Harper 1977; Simberloff 1981; Connell 1983; Schoener 1983; Connolly 1986). Studies examining the form(s) and importance of interspecific competitive interactions are required if we are to understand the role of competition in succession (Drury and Nisbett 1973). In this paper we report on competitive interactions at 3 life history stages between 2 successionally

interacting perennial riparian plant species across a range of ecologically relevant environmental conditions.

Connell and Slayter (1977) presented 3 models of community succession. Successional "facilitation" (primary succession) and "tolerance" models occurred as a result of interspecific competition-based replacement of early successional species by late succession species. The "inhibition" model involved niche preemption by early successional species, with displacement resulting from habitat disruption by disturbance. Sousa (1979b) disputed the non-competitive mechanism of species replacement in the "inhibition" model, finding that competition, not disturbance, resulted in mortality of colonizing algal species. Schoener (1983) considered niche preemption to be a specific form of exploitative (indirect) competition. Huston and Smith (1987) assumed competition was universal among plants and broadened the scope of Connell and Slatyer's (1977) discussion by recognizing that all three mechanisms affect individual plants to a varying degree. Thus interspecific competition may serve as a mechanism in any of the three successional models.

Two general forms of competition (Schoener 1983) serve as mechanisms in the three models of community succession described by Connell and Slayter (1977). These forms of competition include indirect exploitation (e.g., preemption and consumption of resources), and direct interference competition (e.g., allelochemical interaction. Experimental data demonstrating direct interspecific competition among plants are abundant (de Wit 1960; de Wit et al. 1966; Trenbath 1974; Harper 1977; Connell 1983; Schoener 1983); however, pairwise comparisons of species, particularly in laboratory settings, have on occasion lead

to inappropriate conclusions for complex, multi-species field situations (e.g. Kroh and Stephenson 1980).

·Interspecific competition has been considered most influential in highly productive, ecologically stable environments (Weins 1977; Connell 1978; Grime and Hodgson 1987). Riparian ecosystems, including wetlands, are the most biologically productive terrestrial habitats (Warner and Hendrix 1984; Johnson et al. 1985; Mitsch and Gosselink 1986). Flooding disturbance may prevent interspecific competition and limit succession in unregulated riparian settings, except between flooding events and in abandonned channel meanders (Campbell and Green 1968; Johnson et al. 1976). Large dams confer ecological stability on downstream riparian habitats through discharge regulation, and permit a rapid proliferation of riparian vegetation in the newly stabilized habitat (Turner and Karpiscak 1980; Nilsson 1985). Exotic plant species may dominate dam-stablized riparian habitats (Howard and Dolan 1980; Turner and Karpiscak 1980; Nilsson 1985); however, Simberloff (1981) concluded that interspecific competition was rarely implicated in cases of successful invasion by exotic species. Therefore, if interspecific competiton is important, it should be responsible for successional changes in dam-controlled riparian vegetation.

We studied the role of interspecific competition in the successional displacement of exotic Tamarix ramosissima by native Salix exigua in the dam-controlled Colorado River corridor in Grand Canyon National Park, Arizona through a series of field and nursery experiments and surveys. The Colorado River in Grand Canyon was impounded in 1963, and the ecologically stabilized riverbanks were initially colonized by Tamarix. By 1970 native perennial plant species, particularly clonal

Salix _exigua_, began to displace _Tamarix_, a phenomenon not observed elsewhere in the Colorado River basin (P. Martin pers. comm.; Turner and Karpiscak 1980; Brian 1982; Stevens and Waring 1985; Phillips et al. 1987; Stevens 1989). These two species presently co-dominate the riverbanks of Colorado River in Grand Canyon, and both species are extremely flood-tolerant (Stevens and Waring 1985; Stevens 1989). Both plant species grow to small-tree size and typically form dense, monospecific stands, dominating channel margins betweeen 350m and 1,800m throughout the southwestern United States. In addition, both species are perennial deciduous phreatophytes that flower throughout the growing season, and produce minute, wind-dispersed diaspores which require moist, flood-deposited silt beds for germination (Stevens and Waring 1988). Field studies revealed that _Tamarix_ seedlings were common while _Salix_ seedlings were extremely rare in this system, and suggested that establishment never occurred in sites subject to canopy shading (Stevens 1989). _Tamarix_ is an exotic halophyte introduced from southern Asia at the turn of the twentieth century (Robinson 1965) which can produce 2.5×10^8 seeds/year (Stevens 1985). Despite its importance as a phreatophyte and claims of its "aggressive", invasive nature (Johnson 1985; Brotherson and Field 1987), these contentions lack experimental verification. An equally viable alternate hypothesis regarding the success of tamarisk in the Southwest may be that it is more fecund and better adapted to environmental stress in highly disturbed riparian settings than are native species. We experimentally evaluated the successional role of interspecific competition between these species through the germination, seedling and mature age-class life history stages and under various environmental conditions.

Methods

Field, nursery and laboratory experiments and surveys were designed to elucidate aspects of interspecific competition between Tamarix and Salix. Field studies were conducted at Lees Ferry, Arizona (947m elevation) and in the Grand Canyon, and laboratory work was conducted at Northern Arizona University in Flagstaff, Arizona (2,073m elevation).

Field Surveys

A survey of 30 randomly sampled germination sites was conducted in the Grand Canyon by stopping at pre-designated river mileages and searching for the nearest tamarisk seedling in 4 quadrats. Distance to nearest canopy edge was recorded for each seedling at each site.

Rates of rainwater percolation through soils beneath Tamarix and Salix stands to determine if these species differentially modified the soil environments beneath their canopies. Soils beneath these 2 species' canopies were examined 12 hours after a soaking (24 hour) rain at River Kilometer 150 in late October, 1987. Six soil pits were dug to a depth of 50cm beneath Tamarix canopy, Salix canopy and in unvegetated soil. Depth of infiltration was measured in pit. The extent of duff accumulation was recorded in numerous Salix and Tamarix stands throughout the river corridor (Stevens and Waring 1988).

Experimental Methods

Competitive interactions between tamarisk and coyote willow (Salix exigua) were investigated at 3 life history stages several experiments.

Experiment 1: Allelochemical Inhibiton of Germination. Seeds were collected from 12 genets of each species from the Colorado River corridor. Eight 0.5kg samples of 0-2cm surface soil were collected from

beneath the canopies of <u>Tamarix</u>, <u>Salix</u> and from unvegetated soils from throughout the Grand Canyon, were soaked in a 1:1 volume of distilled water for 12 hr, strained and decanted. Seeds of each species were thoroughly mixed and sown at a density of approximately 50 seeds/50cm petri dish in <u>Tamarix</u>, <u>Salix</u> or unvegetated riparian soil leachate. Two replicate seed batches of each treatment were germinated under 1,000klux white flourescent light at 20°C and percent germination measured after 10d. ANCOVA was performed on arcsine-transformed (percent germi-nation)$^{1/2}$ data (Zar 1984), with number of seeds/dish as a covariate.

Experiment 2. Competitive Effects at the Seedling Stage. a) A natural germination event was observed along the banks of the Paria River drainage in June, 1986. Field-collected polygons (plates) of silt containing seedlings of <u>Tamarix</u> and <u>Salix</u> were transferred into 12L pots and thinned to 60 plants/pot (about 1/3 their natural density), with monocultures of 60 <u>Tamarix</u> or 60 <u>Salix</u>, or mixtures with 30 <u>Tamarix</u> and 30 <u>Salix</u> seedlings in each pot. Pots were maintained in an open-air nursery at Lees Ferry and given abundant water (0.5 L/d). Seven replicates of each treatment were maintained for two growing seasons before harvesting.

b) A 2-factor reciprocal field experiment was conducted to determine seedling growth under different canopy types. Laboratory-grown seedling <u>Tamarix</u> and <u>Salix</u> of normal size and vigor were transplanted to the field beneath the canopies of <u>Tamarix</u>, <u>Salix</u>, or neutral shade (55% shade created with lath). Six seedlings of each species were planted in 2 replicates under each canopy type and watered twice weekly for two months, and then monitored for 2 years without additional water.

Experiment 3: Interactions Between Mature Plants. a) A 3-way replacement and density series experiment was designed to test interactions between older age-class plants. Density and proportion were varied from 1:0; 1:1, 2:0; 6:0, 5:1, 3:3 and 1:5 plants of either species/12 L pot, with 10 replicates of each treatment. These densities spanned the range of density found in field surveys (Stevens and Waring 1988). A wide range of genets were used for Tamarix and 10 replicated genets of Salix from throughout the Grand Canyon were used in this experiment. This design followed that of a de Wit (1960) replacement series but also included consideration of density effects (Connolly 1986). Pots were supplied with 0.5 L $\cdot$ d^{-1}, and maintained at Lees Ferry nursery for 3 growing seasons. Relative yield totals were calculated according to Harper (1977).

b) An identical 2-factor reciprocal field transplant experiment to that described in Experiment 2b (above) was conducted to ascertain responses of mature age-class plants of both species to the 3 canopy treatments in Experiment 2b (above). Rooted cuttings of Tamarix and Salix were grown for 2 months in the laboratory and then transplanted to the field.

Experiment 4: Variation in Light and Water. a) Tamarix seedling growth responses to light intensity were examined by sowing tamarisk seeds in 12 L pots of sandy loam under a broad range of light regimes (0.65%, 2.82%, 13.70%, 18.0%, 35.5% and 100% ambient light) at Lees Ferry. Light intensity in this experiment was varied using screens; water was applied at 0.1L/6 hr and 3 replicates of seedlings were grown for 50d before harvesting.

b) To determine the responses of mature individuals to variation in light and water availability, a 3-factor experiment was conducted at an open air nursery at Lees Ferry, Arizona. Two year old tamarisk saplings and 2 year old coyote willow cuttings were collected in the Grand Canyon and were grown in 12 L pots in the open air nursery at Lees Ferry. Experimental plants of each species were randomly assigned to 3 levels of light (4%, 31% and 100%, as measured with a Gossen® light intensity meter) and 3 levels of water (0.25 L/d, 0.5 L/d and 1.0 L/d) in field-collected sandy loam. Eight replicates of the 9 possible treatments (3 light levels x 3 water levels) were maintained for 2 growing seasons and then harvested.

Response Variables and Analyses

Response variables in the above seedling and mature plant growth experiments included: 1) rate of stem length change; 2) total dry biomass accumulation rate in mg/day; 3) dry root:total biomass ratio, a unitless proportion which was transformed by computing arcsine $(R:T)^{1/2}$ for analysis (Zar 1984), and calculated where root separation was possible; and 4) raceme production, again measured where possible. Stem growth and dry biomass accumulation rates provided good measures of performance in a given competitive regime, and dry root:total biomass ratio provided a measure of an individual's proportional allocation of resources to roots as compared to total biomass. Covariates included initial stem mass (wet weight) or stem length. Data were analyzed using ANCOVA (Experiment 1) and MANCOVA (other experiments). Wilk's criterion (Wilk's lambda approximate F), F_W, was reported and univariate F values used where justified by significance level of FW (Johnson and Wichern 1982).

Results

Seedling Surveys

Field surveys revealed that Tamarix was intolerant of shade. The mean distance from a Tamarix seedling to the nearest canopy edge was 3.28m and no Tamarix seedlings were found beneath any canopy plants during the survey. In 3 instances, cohorts of young Tamarix seedlings have been found beneath Tamarix canopies following flooding in the Grand Canyon (Stevens and Waing 1988); however, in none of these cases did any of the thousands of seedlings observed survive more than 6 months.

No Salix seedlings were found during the survey, and fewer than 100 Salix seedlings greater than 0.5yr old have been found in 10 years of observation in this system. Those few Salix seedlings observed were established many metres from the nearest canopy edge.

Substrate Surveys

Vegetation altered soil conditions beneath canopies and increased desiccation stress. Percolation studies demonstrated that infiltration of rainwater was 2.25cm/hr in unvegetated soils, 1.00cm/hr under Salix canopy, and 0.07cm/hr under Tamarix canopies (p = 0.000, df = 2, 15). A total of 4cm of rain fell in 12 hours on 24 October, 1987, yet infiltration beneath dense Tamarix canopy was less than 1cm. The soils beneath Tamarix canopies were virtually hydrophobic, presumably the result of leaching of resins and/or sugars from Tamarix foliage during the summer months.

Duff accumulation was also significant beneath both species, but was greater beneath Tamarix where duff accumulations of up to 150cm were found. Salix duff rarely accumulated to depths exceeding 1cm.

Experimental Results

Germination Responses (Experiment 1). The leachates of Tamarix or Salix surface soils exerted no significant impacts on germination success of either species, as compared to control germinated in leachate from unvegetated soil ($F = 0.386$, $p = 0.818$, df = 2,17; Figure 3.1). Both species' seeds proved to be tiny (ca. 0.1mg dry mass) and both species' seeds germinated in less than 24 hours of moistening at 20°C. Viability of seeds used in this experiment was only moderate because the time required to collect seeds (2 weeks) was approximately 1/3 of the total longevity for these species' seeds. The covariate of seed density/dish was also non-significant ($p > 0.05$, df = 1,17).

Seedling/Seedling Interactions (Experiment 2a). Salix seedlings asymmetrically reduced survivorship, biomass accumulation rate and stem growth rate of Tamarix seedlings ($F_W = 2.372$, $p_W = 0.031$, df = 6,226, with $p < 0.05$ for all 3 responses; Figure 3.2). Tamarix seedling mortality increased from 0% to 6.2% and growth rates decreased from 2.0 mg/d to 0.7mg/d in the presence of Salix seedlings. Salix biomass accumulation rates remained statistically equivalent between monoculture and mixture treatments at 3.9 to 4.0 mg/d.

In Chapter 3 of this dissertation I demonstrated tha proportional allocation to roots (dry root:total biomass ratios) for these 2 species increased when nutrients were limiting. In the present study, allocation varied significantly between species (univariate $p = 0.000$, df = 1,140), but not between monoculture and mixture pot types ($p = 0.356$, df = 1,140). This results indicated that Salix seedlings were not depleting soil nutrients, and that the asymmetrical interaction
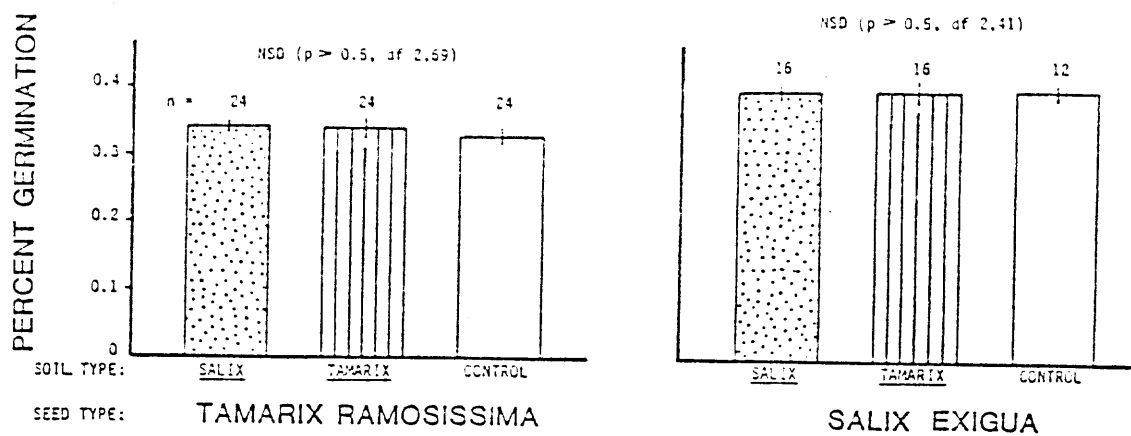
Figure 3.1: Germination success of Tamarix ramosissima and Salix exigua seeds watered with leachates from T. ramosissima, Salix exigua and unvegetated soil from the Grand Canyon. Bars indicate + 1 s.e.
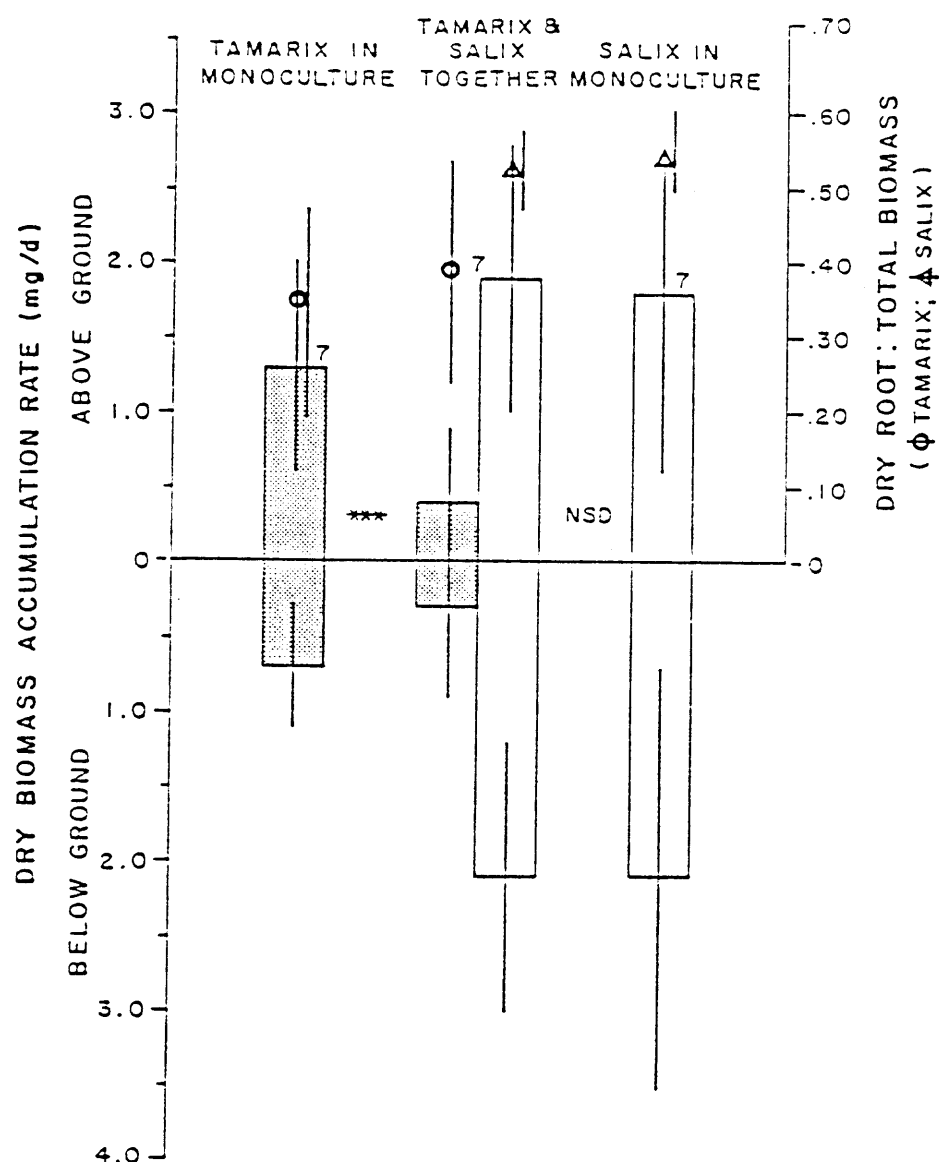
Figure 3.2: Dry biomass accumulation rate (mg/d) and dry root:total biomass ratio of Tamarix ramosissima (shaded bars, circles) and Salix exigua (open bars and triangles) seedlings grown in monoculture and in mixture at a total density of 60 plants/pot for 2 years in an open-air nursery at Lees Ferry, Arizona. Bars are + 1 s.d.

attributed to other factors (e.g. allelochemical or pathogenic interactions).

Adult/Seedling Interactions (Experiment 2b). No Salix seedlings (0 of 36 established seedlings) survived in any canopy setting, while 2 of 36 established Tamarix seedlings survived under neutral shade. Death of experimental seedlings was attributed to desiccation, despite vigorous growth during experimental establishment.

Mature Plant Interactions (Experiment 3a). Density strongly affected growth responses of both species (F_W = 12.284, p = 0.000, df =36,342.8) and species differed significantly in both growth and allocational responses (F_W = 28.346, p = 0.000, df = 4,91; figures 3.3, 3.4). Salix growth rates decreased significantly more between low-density and high-density pots than did Tamarix (Figure 3.3).

Tamarix biomass and stem growth rates were not significantly different across a proportion gradient (p > 0.05) at a density of 6 plants/pot, while Salix biomass and stem growth rates were negatively correlated with proportion (univariate F > 21.9, p = 0.000, df = 6,56 for both; Figure 3.4).

A relative yield total diagram for above ground biomass showed a slight but non-significant (< 10%) decrease in yield of Salix at high Salix proportions, and a non-significant increase in total yield at equal proportions (Figure 3.5).

Proportional allocation to roots was significantly higher for Salix (mean = 0.547) than for Tamarix (mean = 0.382) and did not change significantly with density or proportion/pot (univariate p > 0.05 for both). This demonstrated that the reduction in individual growth across
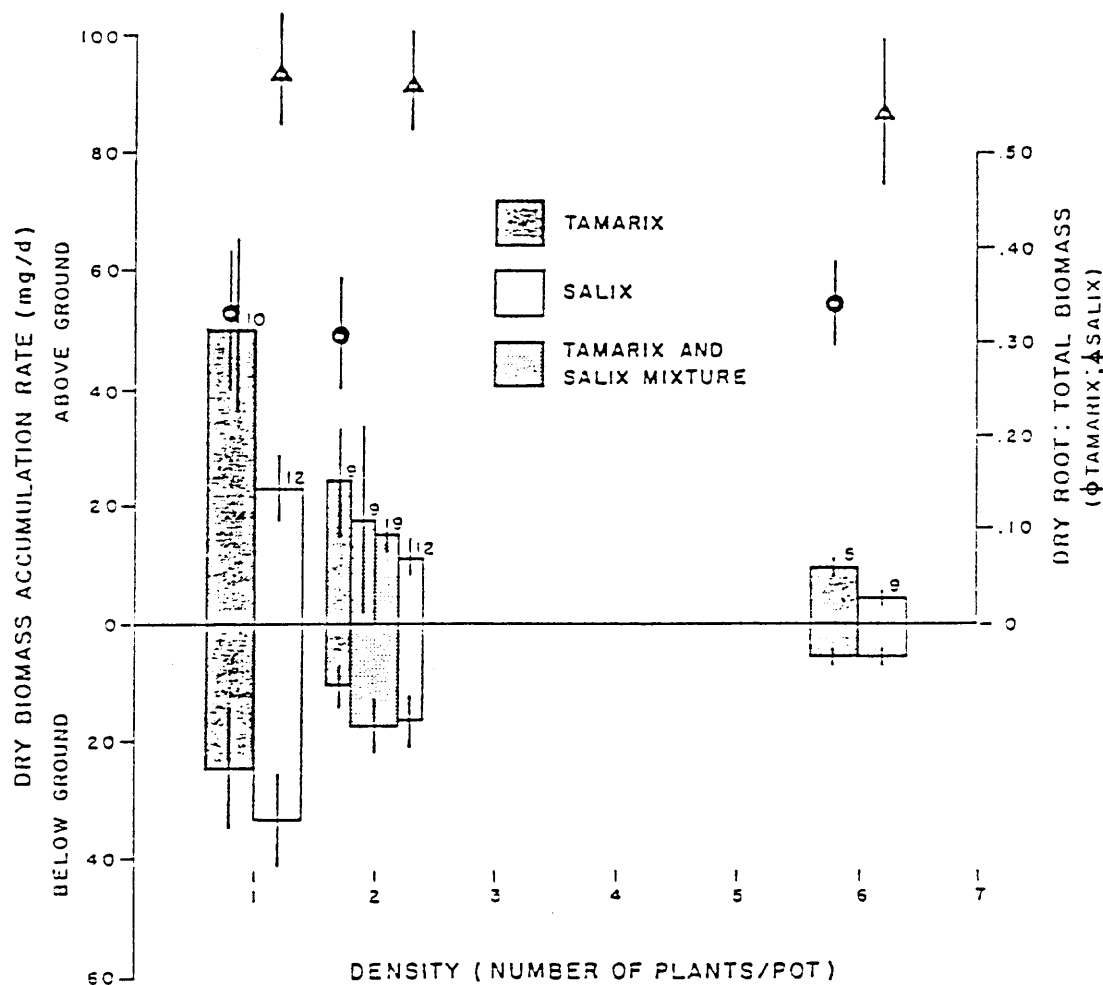
Figure 3.3: Mean dry biomass accumulation rate (mg/d) and mean dry root:total biomass ratio of 4 year old Tamarix (shaded bars and circles) and Salix (open bars and triangles) as a function of density of plants/12L pot. At a density of 2 plants/pot, 3 treatments are shown: 2 Tamarix/pot, 1 Tamarix+1 Salix/pot, or 2 Salix/pot. Bars are ±1 s.d.
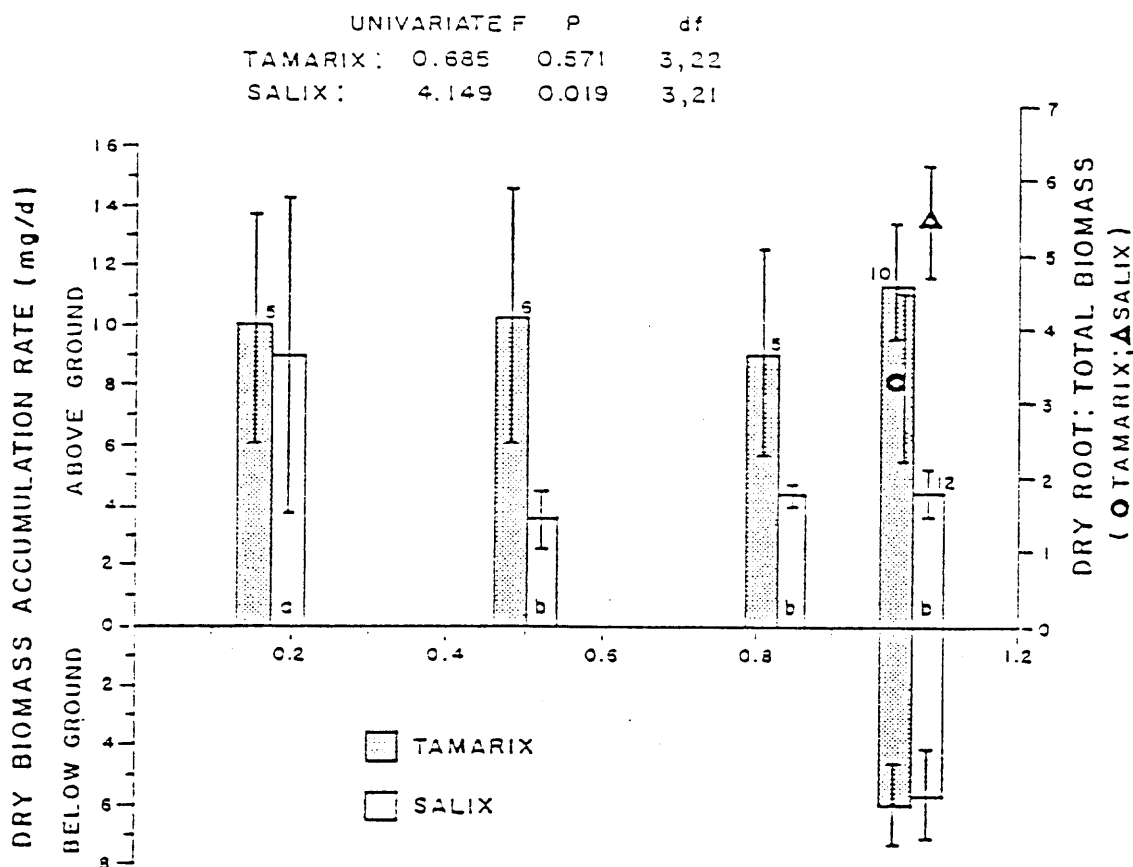
Figure 3.4: Mean dry biomass accumulation rate (mg/d) and mean dry root:total biomass ratio of 4 year old Tamarix (shaded bars and circles) and Salix (open bars and triangles) as a function of proportion/pot. Density was held constant at 6 plants/12L pot. Bars are ± 1 s.d.
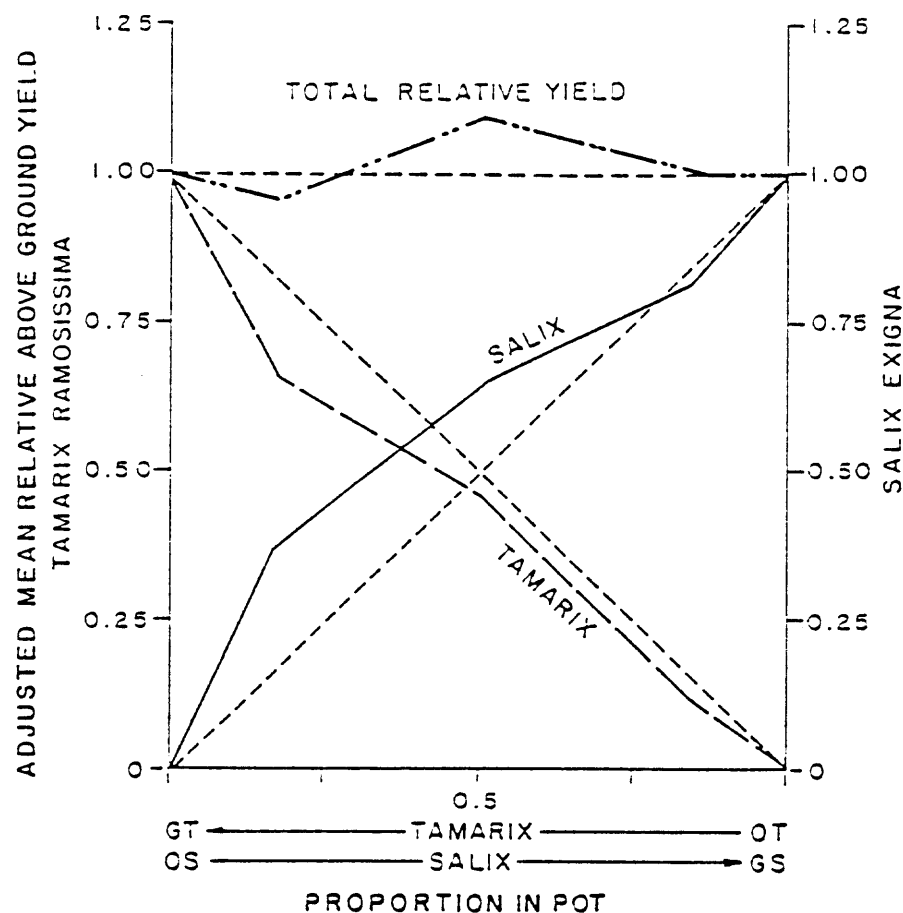
Figure 3.5: Total relative yield diagram (de Wit 1960) for <u>Tamarix</u> and <u>Salix</u> grown in mixtures of 6:0, 5:1, 3:3, 1:5 and 0:6 plants/<u>12L pot</u> for 3 seasons at an open air nursery at Lees Ferry, Arizona. Values on either vertical axis represents the pooled growth of all plants in the pot as a proportion of the growth achienved in monoculture.

the density and proportion (for Salix) gradient may not be caused by nutrient depletion.

Mature Plant Reciprocal Canopy Plantings (Experiment 3b). Tamarix survivorship was significantly higher than Salix ($F = 4.774$, $p = 0.049$, df = 1,12 for pooled transformed percent survivorship). Tamarix survivorship was not significantly different between canopy and non-canopy treatments ($F = 1.025$, $p = 0.388$, df = 2,12). These data and results of numerous other experiments indicated that Tamarix was hardier than Salix.

Seedling Responses to Light Intensity (Experiment 4a). Light intensity was positively correlated with tamarisk seedling growth rates and survivorship in a nonlinear fashion. Ambient light intensity less than 20% ambient strongly curtailed tamarisk seedling growth rates, and survivorship declined to zero below 2.8% ambient light. Maximum stem growth rates occurred at 35.5% ambient light, not under full sunlight ($p < 0.001$, df =5,239), although light intensity was not evaluated between 35% ambient and full sunlight.

Mature Plant Responses to Light and Water. The effects of light and water availability varied significantly between species at the mature-plant stage (Table 3.1). Growth rates were positively correlated with both light and water availability. Salix grew more slowly than Tamarix and responded more strongly to moisture availability (figures 3.6, 3.7), producing significant light x water and species x light interactions. Relative allocation to roots was positively correlated with light availability for both species, but allocation was uncorrelated (Tamarix)

Table 3.1: Mature <u>Tamarix</u> and <u>Salix</u> responses to varied light and water. A MANCOVA analysis using dry biomass accumulation rate (BAR), stem growth rate (SR), and arcsine-transformed (dry root:total biomass ratio)$^{-1/2}$ (RT)] to 3 levels of water (0.25L/d, 0.5L/d and 1.0L/d) and 3 levels of light (4%, 31% and 100% ambient) between mature (3 year old) <u>Tamarix ramosissima</u> and <u>Salix exigua</u> grown for 2 seasons in an open air nursery at Lees Ferry, Arizona.

UNIVARIATE SOURCE	F_W	SIGNIF. OF F_W	DF	SIGNIF. OF TESTS
MAIN EFFECTS:				
Species (S)	8.227	0.000	5,135	BAR**, SR*, RT**
Light (L)	14.730	0.000	10,270	BAR***, RT***
Water (W)	2.350	0.011	10,270	SR***
INTERACTION EFFECTS				
S x L	4.818	0.000	10,270	SR**, RT*
S x W	0.985	0.456	10,270	
L x W	1.819	0.017	20,448	SR*
S x L x W	1.309	0.167	20,448	
COVARIATE EFFECTS				
Initial Stem Mass	0.436	0.496	5,135	

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Tamarix ramosissima
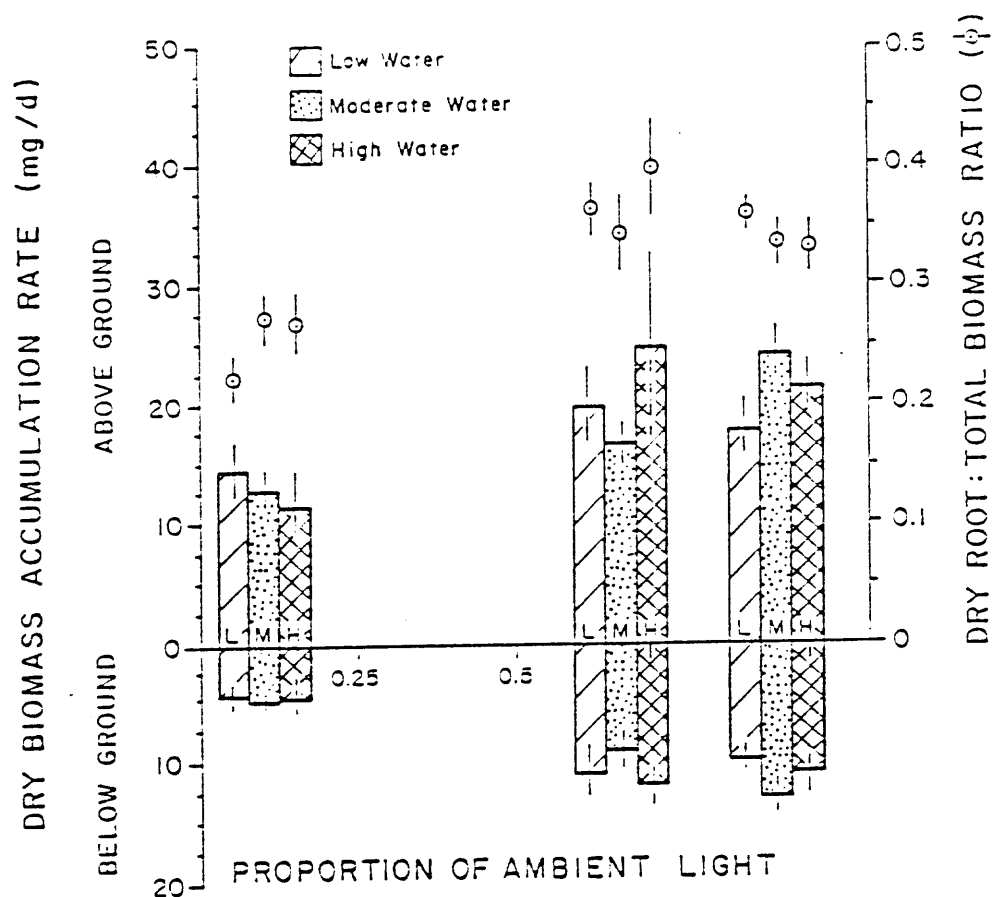
Figure 3.6: Dry biomass accumulation rates (g/d) of 3 year old Tamarix grown under 3 levels of water and 3 levels of light. Eight replicates of each treatment were grown for 2 seasons in an open air nursery at Lees Ferry, Arizona. L = low water, M = moderate water, H = high water. Bars are ± 1 s.d.

Salix exigua
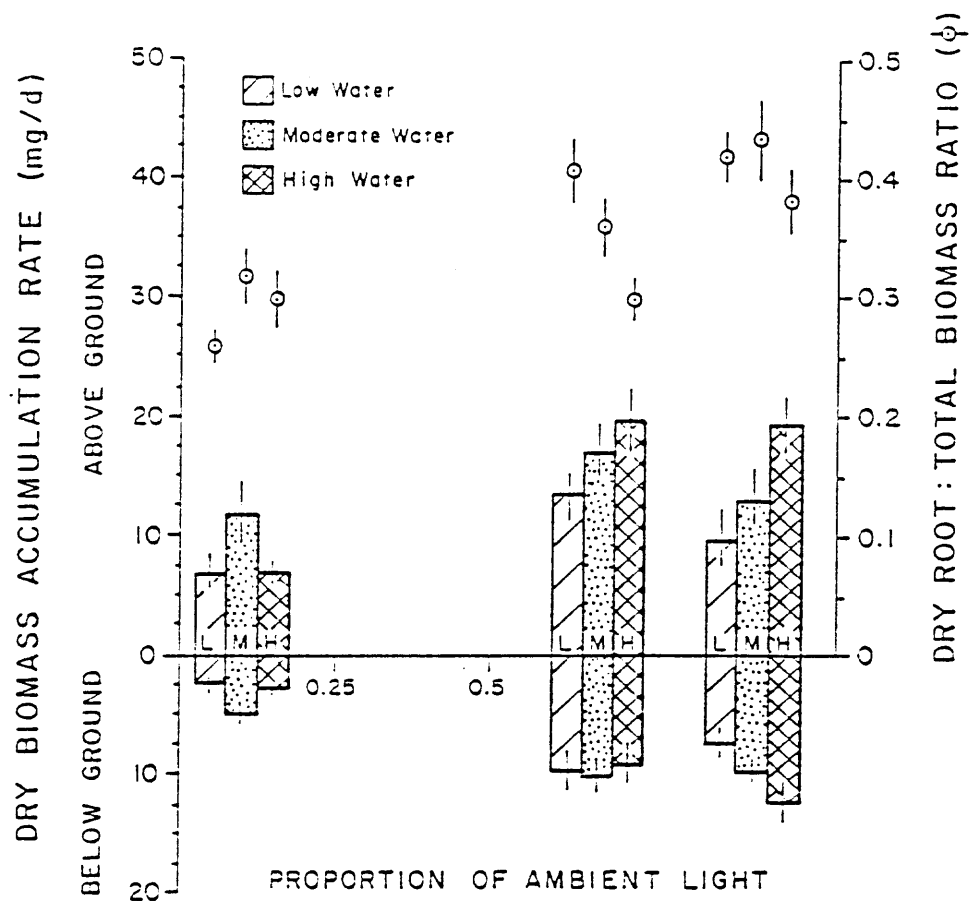
Figure 3.7: Dry biomass accumulation rates (g/d) of 3 year old Salix grown under 3 levels of water and 3 levels of light. Eight replicates of each treatment were grown for 2 seasons in an open air nursery at Lees Ferry, Arizona. L = low water, M = moderate water, H = high water. Bars are ± 1 s.d.

or negatively correlated (<u>Salix</u>) with water availability. All other higher level interaction effects were not significant.

Discussion

This study considered the successional role of competition in a dam-controlled riparian habitat. Direct competition by <u>Salix</u> strongly reduced <u>Tamarix</u> seedling growth rates and survivorship at the seedling stage but not at other life history stages. Despite this strong effect, direct competition was considered unlikely to play a significant role in the successional displacement of <u>Tamarix</u> by <u>Salix</u> because <u>Salix</u> seedings were rare in this system. Succession in the dam-controlled Colorado River riparian corridor took place as the "inhibition" mechanisms of <u>Tamarix</u> (e.g. soil hydrophobitization and duff accumulation) were overcome by the "tolerance" strategies of <u>Salix</u> (e.g., clonal growth and shade tolerance). These results illustrate the case made by Menge and Sutherland (1987) that several successional may modes co-occur simultaneously.

Direct Competition

Neither species directly reduced the germination success of either species' seeds: <u>Tamarix</u> germination was not influenced by soil leachates from either <u>Tamarix</u> or <u>Salix</u>. <u>Tamarix</u> soil hydrophobization, duff accumulation and extreme shading prevented <u>Salix</u> and most other species seedlings from germinating beneath <u>Tamarix</u> canopies. Thus the monocultural nature of <u>Tamarix</u> stands was maintained by inhibition of invasion by other species.

Direct, asymmetrical competitive interaction occurred between these two species at the seedling stage, with <u>Tamarix</u> seedling growth

significantly reduced in the presence of _Salix_ seedlings. Although the timing of the onset of competitive interaction was not investigated here, competitive interactions between seedlings may begin immediately following the rapid germination of these species seeds. In addition to seedling/seedling interactions, seedling mortality was complete beneath mature plant canopies of either species as a result of desiccation. These results support the conclusions of Bradshaw (1987) that the effects of competition vary through life, with the seedling stage being most susceptible to competition. Furthermore, this study supported the contention of Grime and Hodgson (1987) that competition is most important in community organization in highly productive and ecologically stable environments, such as seedling beds.

The causal mechanism in seedling competition appeared to be allelochemical rather than nutrient depletion. Stevens and Waring (1988) documented a strong negative correlation between allocational responses and nutrient availabilty in both _Tamarix_ and _Salix_ seedlings. As nutrient levels increased, proportional allocation to roots decreased. Because relative allocation to roots did not change significantly across either density or proportion gradients in Experiment 3 in either species, reduced growth of seedlings and older age classes appears unrelated to nutrient availability. Competition was probably effected by either allelochemical or possibly by pathogen(s).

The asymmetry of competitive superiority enjoyed by _Salix_ at the seedling stage did not persist among mature plants, where effects on _Tamarix_ were only density-dependent. Mature plants showed no evidence of direct competition although they were grown together at high density for 3 growing seasons. The use of pot and nursery experiments has been

widely criticized; however, if direct competition between mature plants could not be demonstrated under crowded nursery conditions where root interactions were forced, it is improbable that this form of competition could be important in the field.

Tamarix appeared better adapted to desiccation stress and environmental harshness, while Salix appeared better adapted to shading and some aspects of flooding, as indicated by the following observations. 1) Tamarix was generally hardier than Salix under dry conditions and survivorship of Tamarix was higher in all experimental settings except the seedling/seedling competition experiment (Experiment 2a). 2) Both species were flood tolerant, but Tamarix was killed by exposure of the root crown, while Salix responded to root exposure with adventitious root growth (Stevens 1985; Stevens and Waring 1988). 3) Although both species' growth was negatively correlated with light availability, Tamarix was observed in the field to produce few or no seeds when shaded. In contrast, Salix was observed to be reproductively active even in moderate shade. 4) Lastly, Tamarix responded to flooding stress by increasing flower production, while Salix responded to flood stress by increased root production. Thus Tamarix was better able to persist through harsh environmental conditions, while Salix was clonally invasive and indirectly competitive even in shaded canopy settings.

Indirect Competition

Indirect, mechanical forms of competition were important inhibitors of seedling establishment in this system. Tamarix canopy created dense shade, often limiting light to less than 1% of ambient levels (Stevens and Waring 1988). Because both of these species' seedlings are slow-growing as compared to other native riparian perennials, it is not

surprising that seedlings do not persist in shaded settings. Soils beneath _Tamarix_ canopies become coated with foliage resins and/or sugars (Stevens 1985) and become virtually water-proof. This pattern was first observed during extensive soil analyses beneath _Tamarix_ canopies and is negatively correlated with depth in the soil profile (Stevens and Waring 1988). Light limitation, soil hydrophobicity and extensive duff accumulation are primary mechanisms preventing seedling establishment beneath _Tamarix_ canopies. These mechanisms also act beneath _Salix_ canopies, although to a lesser extent.

Succession

Changes in competition effects through life, as well as life history adaptations and other factors influenced successional displacement of _Tamarix_ by _Salix_ in this system. Displacement of _Tamarix_ by _Salix_ in this system was the result of failing "inhibition" of _Tamarix_ (_sensu_ Connell and Slatyer 1977) in which niche preemption by _Tamarix_ was maintained by soil hydrophobicity, duff accumulation and heavy shading, preventing colonization of _Salix_ seedlings. Displacement of _Tamarix_ by clonally-invading _Salix_ resulted from successional "tolerance" by _Salix_ of shading and soil changes under _Tamarix_ canopy. Direct interference competition could not invoked as a causal mechanism driving this successional displacement because _Salix_ seedlings were rare in this system and direct competition between the 2 species occurred only at the seedling stage.

Discharge regulation by Glen Canyon Dam has played a significant role in the successional direction of this system. Relatively stable discharge permitted successional displacement of _Tamarix_ by _Salix_ from 1970 and 1982, and post-dam flooding from 1983 to 1986 upset the course

of that succession by reducing overall diversity and initiating a wide-scale _Tamarix_ germination event (Stevens and Waring 1985, 1988). Under a stabilized discharge regime, _Salix_ may continue to invade _Tamarix_ stands, which are largely incapable of regeneration. By timing spillovers before April, artificial flooding could be used intentionally to shift the dominance from _Tamarix_ to dominance by native species.

CHAPTER 4:

CONSEQUENCES OF DAM-INDUCED SOIL CHANGES
ON RIPARIAN PLANT ESTABLISHMENT IN GRAND CANYON

Introduction

Edaphic change directly influences colonization success and community organization because plant recruitment is rare, probabilistic and depends on substrate quality and propagule availability (Crocker and Major 1955; Grubb 1977; Harper 1977; Nanson and Beach 1977; Grime 1979; Sousa 1979a; Denslow 1980; Spence 1982; Canham and Marks 1985; Tilman 1985, 1988; Fenner 1987; Rorison 1987, Webb et al. 1988). Although pedogenesis has been traditionally considered as a long-term process regulating plant succession through diverse mechanisms (Cowles 1899; Olson 1958; Birkeland 1984), short-term natural and man-caused disturbance of soil characteristics are common and influence recruitment, succession and plant evolution (Antonovics and Bradshaw 1970; Borman and Likens 1979; Denslow 1980; Sousa 1984; Webb et al. 1988). River regulation is a ubiquitous anthropogenic environmental change with construction initiated on 2 or more large dams each day throughout the world (Petts 1984). Impoundment of large rivers abruptly and radically changes the flood disturbance and sedimentation regimes in downstream reaches, stabilizing riverbanks, initiating soil changes and permitting primary colonization by riparian plant life (Johnson et al. 1976; Howard and Dolan 1980; Turner and Karpiscak 1980; Stevens and

68

Waring 1988). Riparian habitats, including wetlands, are important because they are the most biologically productive lands in arid regions, and mismanagment has prompted considerable scientific concern (Johnson and Jones 1977; Warner and Hendrix 1984; Johnson et al. 1985). Although dam-induced riparian soil changes have been documented in regulated river systems, whether and by what mechanisms such changes influence vegetation development is unknown (Stevens and Waring 1988). Detailed studies of the mechanisms influencing plant germination and establishment are generally lacking and would enhance the predictive power of both general and applied ecological theory. The present research was conducted to elucidate mechanisms whereby dam-induced soil changes affected riparian plant establishment.

River regulation has been shown to affect riparian soil quality by coarsening soil texture, leaching nutrients, hydraulic and eolian erosion, desiccation, and by non-renewal of sediment deposits (Turner 1971; Johnson et al. 1976; Turner and Karpiscak 1980; Scala 1984; Van Auken and Bush 1985; Schmidt and Graf 1988; Stevens and Waring 1988). Riparian soils generally consist of young, unweathered, fluvial sediments deposited during subsidence of flood waters (Brock 1985). Although these hydromorphic fluvents, aquents, psamments or haplaquepts generally fall outside the traditional soil classification framework (U.S. Soil Conserv. Service 1975; Brock 1985; Gerrard 1987), fluvial sediment deposits serve as critical germination sites for numerous riparian plant species (Fenner et al. 1984; Stevens and Waring 1985). Riparian soil quality, including moisture availability and as affected by the disturbance regime, has been held responsible for zonation patterns in various riparian plant communities (Johnson 1972;

Johnson et al. 1976; Carothers et al. 1979; Losvik 1983; Anderson and Warren 1985; Brotherson 1987; Inouye et al. 1987).

Recruitment of riparian plants results from differential establishment success in spatially and/or temporally rare "safe" germination sites following flood-induced germination events, with germination and the seedling phase as the most sensitive life history stages (Horton et al. 1960; Warren and Turner 1975; Harper 1977; Fenner et al. 1984; Kozlowski 1984; Reichenbacher 1984; Fenner 1987; Waring and Stevens 1988). Dam-induced changes in riparian soil quality (e.g. changes in texture, nutrient status, pH, water holding capacity) in downstream reaches alter the selection regime acting on seedlings and may differentailly limit recruitment (Grubb 1977). Greater uncertainty of "safe" germination site availability has been predicted to selectively advantage species with greater phenotypic plasticity (Levins 1968; Harper 1977; Crick and Grime 1987; Smith-Gill 1983; Schlichting 1986). Succession in dam-controlled riparian environments may occur in response to differential adaption to changing soil chemistry (Bazazz 1979; Drury and Nisbett 1973; Connell and Slayter 1977; Noble and Slayter 1980).

I explored the impacts of post-dam soil changes on riparian plant recruitment in the Colorado River corridor in the Grand Canyon. Impoundment of the Colorado River by Glen Canyon Dam in 1963 initiated diverse edaphic changes through erosion and non-renewal of riparian soils, coarsening soil texture, decreasing nutrient and mineral status, and increasing pH (Howard and Dolan 1980; Scala 1984; Stevens and Waring 1988). The ecological stability afforded by discharge regulation permitted primary colonization of the riverbanks by riparian plant

species, with initial dominance by <u>Tamarix ramosissima</u> Deneb. and a subsequent increase in dominance of native perennial species, such as <u>Salix exigua</u>, <u>Prosopis glandulosa</u>, <u>Baccharis</u> spp. and <u>Tessaria sericea</u> (Clover and Jotter 1944; Martin, personal communication 1970; Carothers et al. 1979; Turner and Karpiscak 1980; Brian 1982; Stevens and Waring 1985, 1988; Phillips et al. 1987; Pucharelli 1988). Recruitment was found to be relatively rare and was flood-related for most perennial riparian plant species in this system, and clonal species colonized sand beaches more rapidly than species that reproduced primarily by seed (Anderson and Ruffner 1988; Stevens and Waring 1985, 1988). The rapidity of soil change and plant succession in this system, and the correlation between seedling establishment and fine substrates, prompted a study of whether dam-induced changes in soil texture and/or nutrient status differentially influenced the germination and seedling success of common riparian plant species in this system.

Methods

Field Surveys

Field surveys were conducted to determine substrate distribution and habitat requirements of seedlings of the dominant riparian perennial plant species in this system. Substrate distribution was evaluated from 114 2m-wide belt transects between Lees Ferry and Diamond Creek, which ran from the river's edge to the top of the riparian vegetation. Seedling establishment was censused in seven or more 2m x 25m quadrats at the $800m^3$/sec stage (the post-dam river's edge) in each major substrate type (silt, sand, cobble, talus and bedrock), and on 2m

wide belt transects (Figure 4.1). Taxonomy followed that of Phillips et al. (1987), with Tamarix chinensis considered to be T. ramosissima.

Experimental Methods

The effects of soil changes on seedling and sapling growth were assessed in the laboratory and verified in field experiments. Soils used in experiments were collected from representative undisturbed, unvegetated pre-dam fluvial terraces (hereafter referred to as pre-dam soils) and from modern riverside terraces (post-dam soils) at Lees Ferry, Arizona. Soil samples were subjected to standard analyses for pH, base cation and nutrient analyses (Page et al. 1982).

Table 4.1 lists the laboratory and field experiments conducted in this study. Seeds of perennial riparian plant species were collected from 10 or more plants in the Grand Canyon, thoroughly mixed, and germinated for 5 days in distilled water before use, except as noted in Experiment IB.

Experiment IA. Seedling growth responses of 19 common riparian perennials were tested in pre- versus post-dam soil. Seeds of Prosopis glandulosa and Acacia greggii var. arizonica were much larger than those of the other 17 species used and were grown in 3.5cm x 100cm ABS pipe. After one month of growth seedlings were gently flushed from the tubes and measured. The depth of root penetration was observed by inspecting the seedling during the flushing process.

Experiment 1B. Seeds of Baccharis salicifolia were grown individually in 97 samples of various soils from the Colorado River riparian corridor to determine if growth responses were correlated across a wide range of field soil texture.

Figure 4.1: Mean bank profile of the Colorado River in Grand Canyon National Park, Arizona.

Table 4.1: Experimental methods employed in assessing the consequences of dam-induced soil changes.

CONSTRAINT	EXPERIMENT IA	EXPERIMENT IB	EXPERIMENT II	EXPERIMENT III	EXPERIMENT IIIB	EXPERIMENT IV
SOIL TYPE(S)	Pre- vs. post-dam and post-dam soils	Wide range of pre-	Post-dam soil	Post-dam soil	Post-dam soil	Same as IA
PLANT SPECIES	19 spp. (see Table 5)	Past seeds fr/ 1 plant	Tara	Tara, Saex, Iese, Rosl	Same as Expt. IIIA	Tara and Rosl
AGE AT START	5 d	3 d	10 d	8 d	101	60
DURATION OF EXPT.	29-35 d	35 d	30 d	30-31 d	31d	44d
MOISTURE REGIME	At libitum	Same as Expt. IA	0 ml/d, 10ml/d or 20ml/d	10 ml/d	10ml/d	1 1/d, 0.5 1/d, 1.0 1/d
NUTRIENT ADDITION	None	None	0 ml/d, 10ml/d or 20ml/d of Kaufman solution	0.0001 to H,P,K, N,Na,JK,NK,Mne Micronutrs,All	0.001, 0.01, 0.05, 0.101 RKCl	0 or 0.5 1/d Miracle GrO
LIGHT REGIME	16 hr/d of 1,000 klux 1:1 wide spectrum and white flourescent	Same as Expt. IA	16 hr/d of white white flourescent	Same as Expt. II	Same as Expt. II	Direct ambient sunlight
TEMPERATURE REGIME	$25° \pm 2°$ C	Same as Expt. IA	Same as Expt. IA	Same as Expt. IA	Same as Expt. I	Ambient riverside
NO. OF REPLICATES	6 to 25	1 (n = 90)	10	14 or more	21	8
POT TYPE	3.5cm wide x 35 cm tubes	3.5cm Ray 1cm/0 tubes	7cm wide (50ml) pots	Same as Expt. IB	Same as Expt. IB	12 1 pots
EXPT'L DESIGN	2 factor (2 soil, 19 spp.)	Same as Expt. IA 2 water,2 spp.	two-factor (3 nutrs.	One-factor (11 nutr.)	two-factor (4 NaCl, 4 spp)	Field 3 factor (3 water, 3 nutrs., 2 spp.)
RESPONSE VARIABLES (As Growth Rates)	Dry root and shoot mass, length; number of leaves; largest leaf size; dry root:total biomass (p)0.5 trans- formed;	Dry bioass of below and above; number of leaves; largest leaf size; dry root:total bio- mass (arcsine (p).5 transformed	Same as Expt. IB	Same as Expt. IB	Same as Expt. IB	Percent germination, Others as in Expt. IB
ANALYSIS	MANOVA, univariate tests	Same as Expt. IA	Same as Expt IA	Same as Expt. IA	Same as Expt. IA	Same as Expt. IA

Experiment II. A 2-factor laboratory experiment was designed .o distinguish the effects of altered soil texture (decreased moisture retention) and nutrient availability on Tamarix seedling growth. Low (10ml/d) and high (20 ml/d, saturation) deionized water additions, and three levels of nutrients were administered to Tamarix seedlings in field collected, post-dam soil. Experimental variation of water was based on prior evaluation of evaporation rates of post-dam soil in the pot type used in this experiment, with less than 10ml water/d resulting in excessive seedling mortality. The high nutrient dosage was a full strength Kaufman et al. (1975: 130) solution consisting of 5.0ml 1M $Ca(NO_3)_2$ + 5.0ml 1M KNO_3 + 2ml 1M $MgSO_4$ + 1.0ml 1M KH_2PO_4 + 1.0ml 1M FeEDTA + 1.0ml micronutrient solution brought to 1 liter volume with deionized H_2O. The medium concentration nutrient solution was one half of the full strength concentration, and the low nutrient treatment was simply deionized water added to post-dam soil. Measured nutrient solutions were delivered in daily water treatments to assure continuous nutrient availability.

Experiment IIIA. To determine which nutrients were limiting, Tamarix, Salix exigua, Tessaria sericea and Baccharis salicifolia seedlings were grown one each in 3.5cm-growth tubes with 10ml/d of 0.001M N (as nitrate), K, P, Fe, micronutrients, NP,PK,NK,NPK and control plants received Kaufman et al. (1975) complete hydroponic solution or just deionized water.

Experiment IIIB. The effects of soil salinity on seedling growth were examined for the same four dominant species by adding daily water containing 0.00M, 0.01M, 0.05M or 0.10M NaCl to growth tubes of post-dam

soil containing 1 individual/species (21 replicates each). These levels of salinity were selected to bracket the differences between pre-dam and post-dam soil conditions.

Experiment IV.   To determine if conclusions on the role of moisture retention and nutrient status drawn from laboratory tests were supported in the field, a 3-factor experiment was designed to examine the effects of soil texture and nutrient status on germination and seedling growth rates between Tamarix and Baccharis salicifolia at Lees Ferry, Arizona.   Two hundred Tamarix seeds and 100 B. salicifolia seeds were sown in 12 L pots filled with pre-dam, post-dam or fertilized post-dam soil at the riverside.   Full strength Miracle-Gro® solution was applied $0.5L \cdot wk^{-1} \cdot pot^{-1}$ to appropriate pots.   Water treatments consisted of high ($0.33L \cdot 8hr^{-1} \cdot pot^{-1}$), medium ($0.17L \cdot 8hr^{-1} \cdot pot^{-1}$), or low ($1.0L \cdot wk^{-1} \cdot pot^{-1}$) dosages.   Pots were open at the base and were buried to the rim in the ground at the water's edge to maintain natural soil humidity levels and were exposed to full summer sunlight. Germination was evaluated after 10 days.   Seedlings were then thinned to 30 plants of each species/pot and harvested at 40 days.

Analyses

Response variables in growth experiments included: 1) the total dry biomass accumulation rate (mg/day), which provided a general indication of overall plant performance in a soil type; and 2) the dry root:total biomass ratio (R:T), transformed by computing arcsine $(R:T)^{1/2}$ for analysis (Zar 1984), which provided a measure of a seedling's proportional allocation of resources to roots as compared to above-ground biomass.   In Experiment 1A, rates of descent of roots into the

soil (cm/day), leaf growth (cm^2/d) and production (number/d), and stem growth (cm/d) were also measured.

Comparative R:T responses in pre-dam versus post-dam soils were used to generate an index of allocational plasticity for each plant species:

$$API_i = \text{arcsine } [(\Sigma R:T_i)/n_{i_{post}}]^{1/2} - \text{arcsine } [(\Sigma R:T_i)/n_{i_{pre}}]^{1/2}$$

where API_i was the allocational plasticity index for species i; $R:T_i$ was the dry root:total biomass ratio for species i in post-dam or pre-dam soil; and n_i was the sample size of species i. API_i values varied from less than -0.1 (greater relative allocation to roots in pre-dam soil) through 0 (low phenotypic plasticity) to 0.4 (high phenotypic plasticity), and this index provided a useful measure of a species' ability to adjust to dam-induced soil changes. Data from 'the above experiments were analyzed using MANOVA with multiple response and predictor variables, with univariate analyses where justified by multivariate results. Wilk's lambda approximate F and significance levels (referred to in the results as F_W and p_W, respectively) are derived from Wild's criterion, a commonly used likelihood ratio statistic employed to detect differences between sample means in a multivariate context (Johnson and Wichern 1982).

Results

Field Surveys of Substrate and Seedling Distribution

Silt-rich substrates were relatively rare in the river corridor, comprising only 9.5% of the terrace below the 1,130 m^3/sec stage and

2.5% of terraces between the 1,130 and 1,700 m^3/sec stages in 1987 (Table 4.2). Sand comprised 19.6% and 19.4% of the surface area in these two lower floodzones, respectively, and coarser substrates (gravel, cobble, brecchia and especially bedrock) dominated the system overall.

Seedlings, especially those of $\underline{T. \; ramosissima}$, were significantly more abundant in silt deposits than in sand at the water's edge (below the 850m^3/sec stage): 68.4% of 57 silt deposits were heavily colonized by seedlings, whereas only 6.9% of coarse 44 sand deposits were colonized (X^2 = 43.65, p < 0.001, df = 1). Only clonally spreading species such as $\underline{Salix \; exigua}$, $\underline{Tessaria \; sericea}$ and $\underline{Aster \; spinosus}$ were abundant on coarse sand deposits. Log_{10}-transformed seedling density and untransformed species richness were significantly greater in silt-rich substrates, as compared to sand or other substrate deposits (F_W = 13.555, p = 0.000, df = 8,86; Table 4.3). Univariate analyses revealed significantly higher seedling density in silt as compared to sand and coarser substrates (p < 0.001, df = 4,44). Species richness of seedlings was significantly lower in silt and sand substrates than in coarser substrates and was highest in cobble substrates (p = 0.001, df = 4,44). Two-way analysis of variance demonstrated significant differences and interaction in seedling density between floodzones and species, with significantly higher seedling density on the <1,130 m^3/sec (mean seedling density of all species pooled = 2.78/m^2) than on the 3,550m^3/sec terrace (0.33/m^2; Figure 4.2). Significant interaction between zones and species was due to different distribution patterns between species. $\underline{Tamarix}$, $\underline{Salix \; gooddingii}$ and $\underline{Baccharis}$ spp. seedling abundance decreased on upper terraces, while $\underline{Brickellia \; longifolia}$ and

Table 4.2: Substrate particle size frequency and relative areal extent. Floodzones (stage in m^3/sec) were sampled in the Colorado River riparian corridor in Grand Canyon National Park, Arizona. Sample size (n) refers to the total number of transects/zone dominated by a given substrate type.

APPROXIMATE FLOOD-ZONE STAGE (m^3/sec)	PROPORTION OF SUBSTRATE WITHIN A FLOODZONE (n)					
	SILT	SAND	FINE GRAVEL	COARSE GRAVEL	COBBLE OR TALUS BRECCHIA	BEDROCK
< 1,130	0.0950 (9)	0.1958 (17)	0.2236 (13)	0.2240 (18)	0.1588 (24)	0.1028 (33)
1,130 - 1,700	0.0253 (4)	0.1938 (12)	0.2572 (12)	0.2239 (23)	0.1580 (22)	0.1419 (40)
1,700 - 2,550	0.1037 (11)	0.1166 (9)	0.2378 (9)	0.1446 (17)	0.1641 (20)	0.2333 (47)
2,550 - 3,550	0.1057 (15)	0.1629 (10)	0.1918 (11)	0.1824 (21)	0.1846 (17)	0.1726 (40)
> 3,550	0.2669 (17)	0.1351 (5)	0.1347 (13)	0.1325 (15)	0.0691 (11)	0.2617 (48)
TOTAL	0.1382 (56)	0.1614 (53)	0.1987 (58)	0.1790 (94)	0.1359 (94)	0.1868 (208)

Table 4.3: Riparian seedling diversity by substrate texture and stage. Density and species richness of riparian perennial plant seedlings in 5 substrate types throughout the Colorado River corridor, Grand Canyon National Park, Arizona. MANOVA of arcsine $(p)^{1/2}$ - transformed (seedling density), and species richness, $F_W = 13.555$, $p < 0.001$, $df = 8,86$.

SUBSTRATE TYPE	NO. PLOTS SAMPLED	MEAN SEEDLING DENSITY/m^2 (S.D.)*	MEAN SEEDLING SPECIES RICHNESS (S.D.)*
Silt	7	3,314.4 (4,364.9)[a]	1.86 (1.4639)[ab]
Sand	11	9.9 (12.9727)[b]	1.18 (1.1677)[a]
Cobble	13	35.6 (26.6913)[c]	4.92 (2.3260)[c]
Talus Brecchia	9	45.1 (40.9678)[c]	3.89 (2.3688)[bc]
Bedrock	9	11.8 (8.7146)[bc]	3.11 (1.1667)[abc]

* Univariate oneway AOV range tests groupings using $\log_{10}$ transformed abundance and untransformed species richness data.

SPECIES

1 — TAMARIX RAMOSISSIMA
6 — SALIX GOODDINGII
8 — BACCHARIS SALICIFOLIA
9 — BACCHARIS EMORYI
12 — BRICKELLIA LONGIFOLIA
18 — HAPLOPAPPUS ACRADENIUS

F = 5.493
p < 0.001
df = 5,216
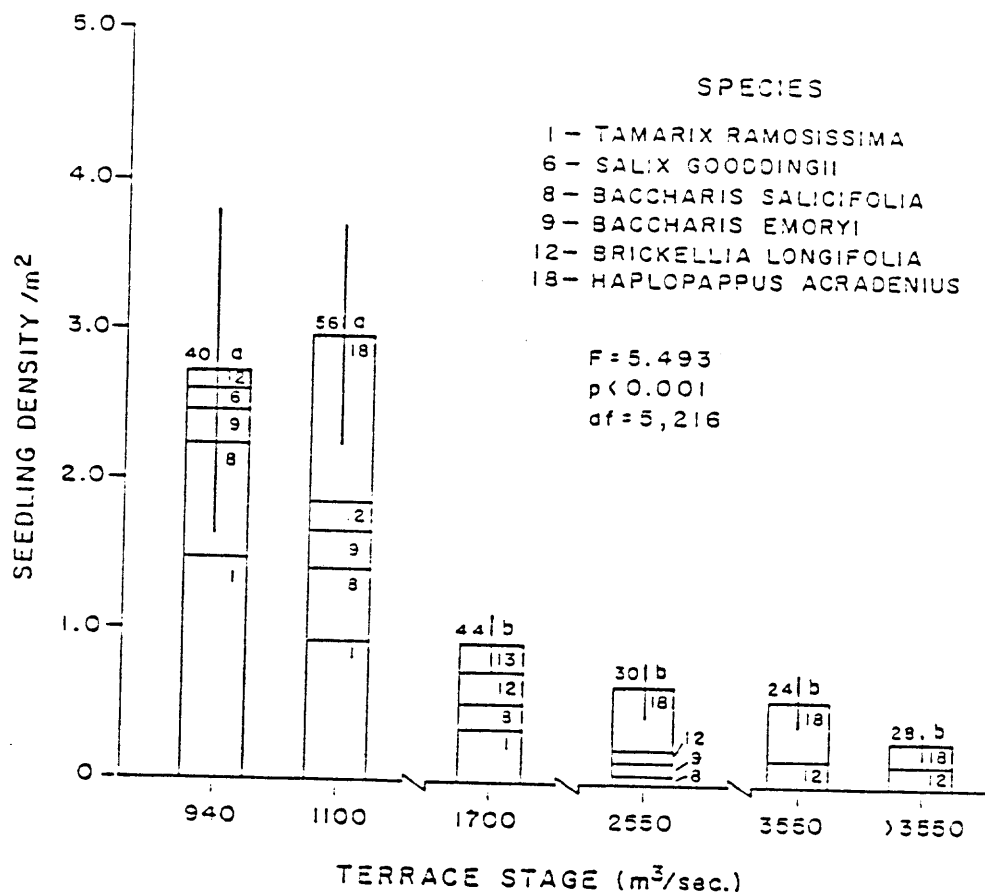
Figure 4.2:   Densities/m^2 of common perennial riparian plant species'
seedlings on channel margin terraces in the Colorado River riparian
corridor in the Grand Canyon.   MANOVA analyses revealed significant
differences were found between terraces (FW = 2.765, pW = 0.020, df =
5, 190; letters indicate univariate SNK range test results) and between
species (FW = 6.991, pW < 0.001, df = 5,190), and interaction effects
were significant (FW = 1.730, pW = 0.032, df = 20, 190).

<u>Haplopappus</u> <u>acredinius</u> only occurred on upper terraces. Ramet density of the dominant clonal species (<u>S</u>. <u>exigua</u>, <u>Alhagi</u> <u>camelorum</u>, <u>Aster</u> <u>spinosus</u> and <u>Tessaria</u>) was not significantly different between zones (p = 0.744, df = 5,80); however, species composition shifted from dominance by <u>Salix/Tessaria</u> to <u>Tessaria/Aster/Alhagi</u> on upper terraces.

In summary, field surveys demonstrated that: 1) silt substrates were rare and were most subject to future flooding disturbance; 2) seedling density was significantly greater in relatively rare deposits of silt as compared to sand or other substrates; 2) seedling abundance was correlated with proximity to the river; and 3) perennial riparian species were unequally represented in seedling beds, with <u>Tamarix</u> most abundant at the water's edge.

Effects of Pre-dam Versus Post-dam Soil on Seedling Growth

Soil analyses showed decreased nutrient, salinity and base cation concentrations, decreased fine (silt-clay) fraction and drying rate, and increased pH and infiltration drying rate in post-dam soils, as compared to pre-dam soils (Table 4.4). Characteristics of soils used in the experiments were moderately different, not extremes decribed in the system by Stevens and Waring (1988).

Seedling growth responses were significantly reduced in post-dam soil as compared to pre-dam soil, except R:T which increased significantly in post-dam soil (Table 4.5, Figure 4.3). All growth parameters varied significantly between soils (p_W = 0.000; df = 4.00,321.00; Figure 4.3), with a grand mean total dry biomass accumulation rate in pre-dam soil of 1.19 mg/d versus 0.71 mg/d in post-dam soil. Growth rates varied significantly between species (p_W = 0.000, df = 72.00,1264.61), with univariate p values all < 0.01, df =

Table 4.4: Edaphic characteristics of soils used in laboratory and field experiments.

SUBSTRATE PARAMETER	PRE-DAM SOIL	POST-DAM SOIL
pH	8.1	8.8
K^+ (ug/g)	213.7	19.3
Na^+ (ug/g)	393.6	41.3
Mg^{2+} (ug/g)	229.6	75.7
Ca^{2+} (ug/g)	1695.0	666.7
Total Base Cations (ug/g)	2531.9	803.0
NO_3^- (ug/g)	18.5	7.2
PO_4^- (uf/f)	3.7	2.7
Percent Sand	89.0	97.0
Percent Silt+Clay	11.0	3.0
Infiltration Rate (cm/min.)	1.08	3.13
Soil Density (g/ml soil)	1.31	1.48
Percent Pore Space	28.9	22.0
Drying Rate (hrs at 43°C)	200	162

Table 4.5: Growth characteristics (rates of root growth, total dry biomass accumulation, leaf addition and proportionate allocation to roots as arcsine $(p)^{1/2}$ for seedlings of 19 perennial plant species grown in pre-dam versus post-dam riparian soil from Grand Canyon.[*]

SPECIES	SOIL TYPE	MEAN ROOT ELONGATION RATE cm/d (n,sd)	MEAN DRY BIOMASS ACCUMULATION RATE mg/d	MEAN DRY ROOT:TOTAL BIOMASS RATIO	MEAN LEAF ADDITION RATE no./d	MEAN LEAF GROWTH RATE cm²/d
Tamarix ramosissima	Pre-dam	0.410 (12, 0.129)	0.199 (0.116)	0.507 (0.144)	0.145 (0.076)	----
	Post-dam	0.370 (12, 0.124)	0.183 (0.172)	0.786 (0.124)	0.062 (0.088)	----
Salix exigua	Pre-dam	0.525 (7, 0.274)	0.197 (0.144)	0.332 (0.108)	0.254 (0.047)	0.016 (0.012)
	Post-dam	0.402 (14, 0.151)	0.222 (0.152)	0.691 (0.102)	0.220 (0.033)	0.008 (0.005)
Salix goodingii	Pre-dam	0.256 (10, 0.078)	0.068 (0.027)	0.535 (0.081)	0.115 (0.023)	0.004 (0.003)
	Post-dam	0.643 (13, 0.119)	0.108 (0.033)	0.518 (0.121)	0.170 (0.039)	0.008 (0.003)
Baccharis salicifolia	Pre-dam	0.290 (20, 0.249)	1.155 (0.929)	0.485 (0.121)	0.297 (0.118)	0.088 (0.048)
	Post-dam	0.583 (11, 0.135)	0.405 (0.229)	0.838 (0.044)	0.225 (0.023)	0.013 (0.006)
B. emoryi	Pre-dam	0.203 (10, 0.278)	1.497 (0.561)	0.409 (0.073)	0.337 (0.072)	0.093 (0.038)
	Post-dam	0.565 (10, 0.069)	0.177 (0.059)	0.502 (0.102)	0.197 (0.051)	0.011 (0.003)
B. sergiloides	Pre-dam	0.731 (10, 0.193)	0.409 (0.107)	0.385 (0.075)	0.336 (0.075)	0.027 (0.009)
	Post-dam	0.511 (11, 0.188)	0.174 (0.038)	0.507 (0.073)	0.225 (0.020)	0.011 (0.002)
B. sarothroides	Pre-dam	1.048 (10, 0.266)	2.423 (1.018)	0.463 (0.073)	0.613 (0.171)	0.140 (0.019)
	Post-dam	0.516 (11, 0.095)	0.538 (0.155)	0.667 (0.057)	0.252 (0.040)	0.019 (0.006)
Brickellia longifolia	Pre-dam	0.383 (6, 0.224)	2.737 (1.579)	0.425 (0.081)	0.839 (0.260)	0.153 (0.069)
	Post-dam	0.875 (5, 0.235)	0.528 (0.327)	0.570 (0.113)	0.312 (0.063)	0.029 (0.014)
Haplopappus acredenius	Pre-dam	0.494 (11, 0.111)	0.605 (0.120)	0.500 (0.054)	0.249 (0.023)	0.028 (0.007)
	Post-dam	0.442 (10, 0.215)	0.262 (0.244)	0.537 (0.134)	0.211 (0.035)	0.012 (0.005)
Prosopis glandulosa	Pre-dam	0.993 (13, 0.393)	3.695 (1.779)	0.250 (0.053)	0.247 (0.019)	0.007 (0.002)
	Post-dam	0.835 (12, 0.233)	3.078 (1.186)	0.409 (0.169)	0.233 (0.037)	0.005 (0.003)
Acacia greggii	Pre-dam	0.966 (12, 0.436)	3.687 (1.952)	0.291 (0.148)	0.339 (0.138)	0.007 (0.003)
	Post-dam	0.640 (14, 0.300)	4.095 (1.478)	0.328 (0.182)	0.292 (0.122)	0.005 (0.002)
Populus fremontii	Pre-dam	0.845 (9, 0.247)	3.298 (1.632)	0.637 (0.136)	0.262 (0.035)	0.194 (0.105)
	Post-dam	0.553 (10, 0.154)	0.723 (0.418)	0.504 (0.176)	0.197 (0.019)	0.025 (0.011)
Fallugia paradoxa	Pre-dam	0.460 (10, 0.173)	0.199 (0.069)	0.316 (0.103)	0.203 (0.035)	0.022 (0.009)
	Post-dam	0.533 (5, 0.145)	0.194 (0.028)	0.267 (0.028)	0.199 (0.013)	0.020 (0.004)
Aster spinosus	Pre-dam	0.174 (10, 0.132)	0.062 (0.029)	0.547 (0.172)	0.147 (0.028)	0.006 (0.003)
	Post-dam	0.312 (10, 0.125)	0.071 (0.039)	0.598 (0.080)	0.153 (0.016)	0.005 (0.002)
Tessaria sericea	Pre-dam	0.787 (12, 0.212)	0.929 (0.725)	0.461 (0.104)	0.363 (0.100)	0.075 (0.031)
	Post dam	0.605 (12, 0.258)	0.415 (0.377)	0.743 (0.066)	0.215 (0.041)	0.024 (0.016)
Phragmites australis	Pre-dam	0.486 (13, 0.154)	0.767 (0.713)	0.552 (0.109)	0.154 (0.035)	0.028 (0.013)
	Post-dam	0.375 (9, 0.114)	0.098 (0.055)	0.721 (0.090)	0.107 (0.015)	0.014 (0.005)
Typha latifolia	Pre-dam	0.073 (17, 0.022)	0.007 (0.001)	0.471 (0.066)	0.100 (0.000)	0.002 (0.002)
	Post-dam	0.113 (23, 0.019)	0.019 (0.010)	0.478 (0.149)	0.100 (0.000)	0.016 (0.005)
Typha domingensis	Pre-dam	0.029 (2, 0.004)	0.019 (0.002)	0.452 (0.168)	0.057 (0.000)	----
	Post-dam	0.024 (2, 0.010)	0.009 (0.004)	0.500 (0.000)	0.029 (0.000)	----
Fraxinus pennsylvanica	Pre-dam	0.439 (9, 0.123)	0.662 (0.239)	0.492 (0.079)	0.141 (0.022)	0.036 (0.010)
	Post-dam	0.493 (11, 0.103)	0.620 (0.167)	0.346 (0.072)	0.175 (0.033)	0.061 (0.030)

[*] See text for MANOVA results.

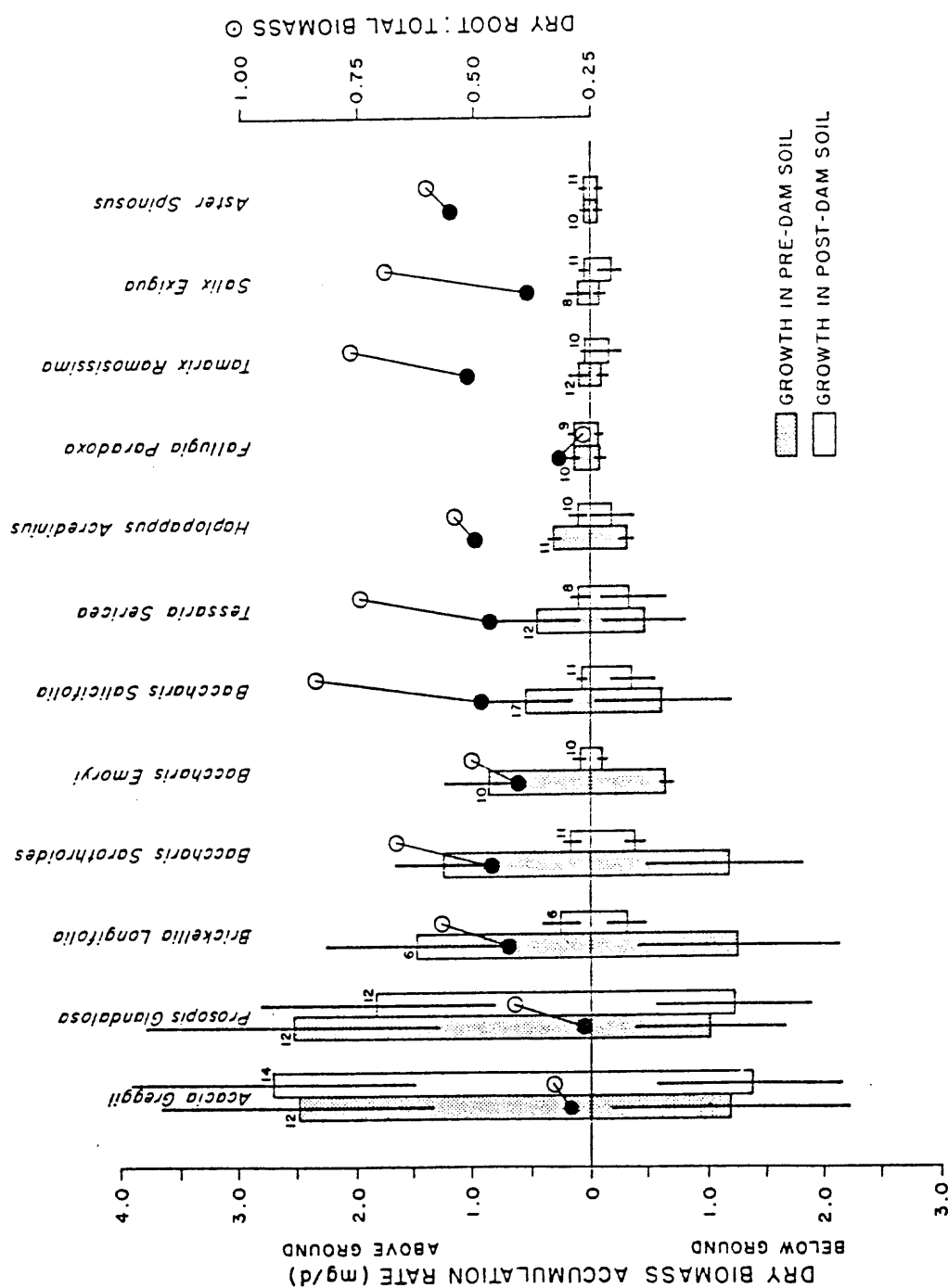Figure 4.3: Dry biomass accumulation rates (mg/d) and dry root:total biomass ratios of 12 common riparian plant species in pre-dam versus post-dam soil from the Grand Canyon. Note that most, but not all species' root:total ratios (circles) increased in nutrient poor post-dam soil. Significant differences were noted between soil types ($p_W=0.000$, df = 4,321) and between species ($p_W=0.000$, df = 72,1265).

1,324). Slow mean growth rates were characteristic of Tamarix, S. exigua, Typha spp. and Fallugia paradoxa; intermediate growth rates were observed in Phragmites australis, Baccharis sergiloides, and Haplopappus acradenius; and highest growth rates were observed in Prosopis glandulosa, Acacia greggii, Baccharis salicifolia, B. sarothroides, B. emoryi and Brickellia longifolia. Significant interaction effects between soil types and species were attributed to non-equivalent responses by some species to the two soil types (p_W = 0.000; df = 72.00,1264.61). For example, Tamarix, S. exigua, and Baccharis spp. growth rates were 3 to 4 times greater in pre-dam than in post-dam soil, while Typha spp., Acacia, Prosopis and Populus fremontii growth rates did not differ significantly between the two soil types. Experiments confirmed that all species were capable of surviving for more than one month in post-dam soil in the laboratory.

Root growth rates were lower in post-dam soils among most, but not all of the species' seedlings examined (univariate p = 0.000, df = 1,324; Table 4.5). Significant between-species differences were found in root growth rates ($p_{univariate}$ = 0.000, df = 18,324) with absolute root depth achieved by one month old Acacia, Prosopis, Baccharis salicifolia, B. sarothroides, and B. emoryi seedlings significantly greater than those of Tamarix, S. exigua or Typha spp. The root of one 30 day old Acacia seedling exceeded 50cm in depth in pre-dam soil, while mean Typha latifolia L. root length was only 2.19cm (0.073cm/d) in the same soil type. Likewise, the number of leaves/seedling and the size of the largest leaf were generally, but not always, significantly greater on seedlings grown in pre-dam soil, as compared to those grown in post-dam soil (Table 4.5).

Proportional allocation to roots (arcsine $(p)^{1/2}$ transformed dry root:total biomass ratio) varied significantly between soil types and between species (Table 4.5; Figure 4.3), with the greatest relative response to soil type in Tamarix, Baccharis salicifolia, Tessaria, and S. exigua. Acacia, Prosopis, Populus fremontii and F. paradoxa root growth rates were not significantly different between soil types, resulting in a significant interaction effect between soil type and species (univariate $p = 0.000$, d.f. = 18,324).

The correlation between seedling growth rate and soil quality was confirmed for numerous pre-dam and post-dam soils in Experiment IB ($p_W = 0.000$, df = 4, 184 for $\log_{10}$ transformed growth rate data). Mean dry biomass accumulation rate of B. salicifolia seedlings grown in post-dam soil was 0.0498 mg/d (n=47, sd = 0.058), significantly lower than that of seedlings grown in pre-dam soil (0.0179 mg/d, n = 42, sd = 0.022; $p_{univariate} = 0.008$, df = 2,97). Mean seedling growth rate in recently aggraded sediments was significantly larger than in pre-dam soil (mean = 0.161mg/d, n = 9). The effects of soil pH were not significant ($p_W = 0.409$, df = 2,184).

Allocational Plasticity

Seedlings of species that exhibited strong allocational plasticity (e.g. Tamarix, B. sarothroides, B.salicifolia; and young ramets of clonal S. exigua, Tessaria and Phragmites australis) were significantly more common than species which were less capable of altering allocation between roots and above-ground growth (e.g. Populus fremontii, S. gooddingii Ball. and Fraxinus pennsylvanica. Log10 seedling abundance in 1987 was significantly and positively correlated with API ($R^2 = 0.427$, F = 12.660, p < 0.005, df = 1,17; Figure 4.4).
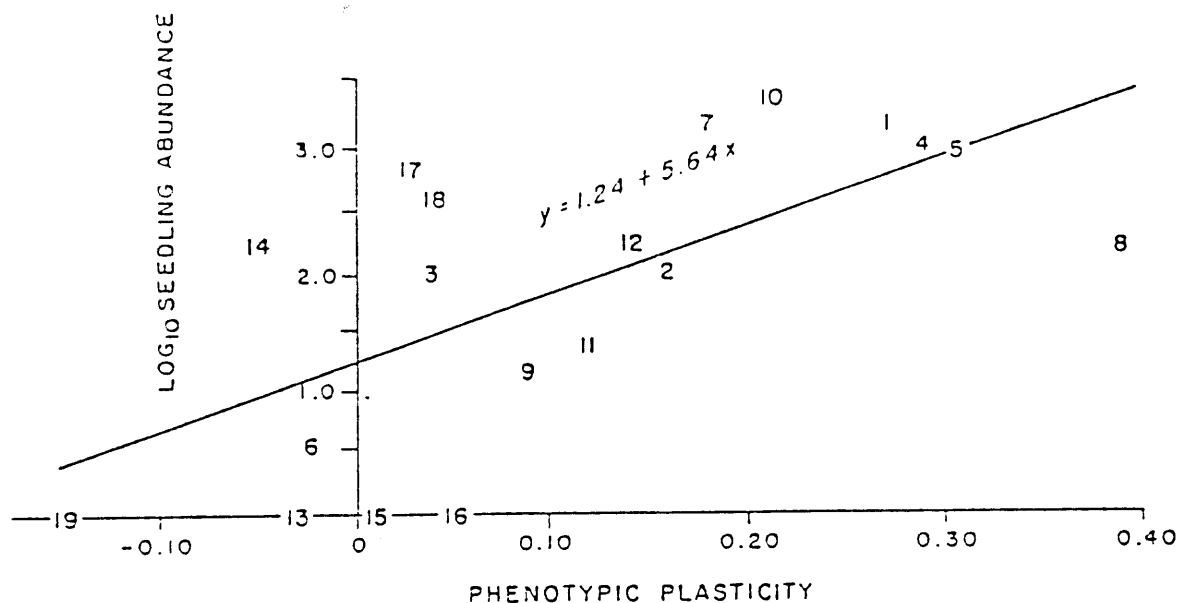
Figure 4.4: Log10-transformed seedling abundance by species (numbers) as a function of allocational plasticity in the Colorado River riparian corridor in the Grand Canyon. Numbers are species' identification numbers listed in Table 4.5. This figure shows that a species' allocational plasticity was correlated with abundance of that species' seedlings in the field (regression equation: log10 (y) = 1.24 + 5.64 x; R^2 = 0.427, p < 0.005, df = 1,17).

Water Versus Nutrient Availability

Tamarix seedlings responded significantly to both nutrient and water augmentation in the laboratory (Figure 4.5). Univariate analyses demonstrated that nutrient addition significantly decreased relative allocation to Tamarix seedling roots (p = 0.027, df = 2,52) but not total dry biomass accumulation rate (p = 0.672), while soil saturation significantly decreased both total biomass accumulation rate and allocation to roots (p = 0.003 and 0.000, df = 1,52, respectively). Interaction effects between water and nutrient availability were not statistically significant.

Nutrient Additions in the Laboratory

Four dominant species' seedlings grown in post-dam riparian soil in the laboratory demonstrated complex and significant differences in growth patterns between nutrient treatments (F_W = 39.532, p = 0.000, df = 42,2596) and between species (F_W = 20.387, p_W = 0.000, df = 9, 2130), and interaction effects were also significant (F_W = 12.452, p = 0.000, df = 120, 2622). Covariate effects of pH were not significant (p_W = 0.676, df = 3, 875). Tamarix seedlings had the lowest overall growth rate, and responded strongly to all additions of N, including N, NP, NPK and complete nutrient additions. S. exigua seedlings responded strongly to K and micronutrient additions. B. salicifolia responded only to the various nutrient additions containing NP. Tessaria sericea seedlings responded to PK additions. Relative allocation to roots decreased among all species as limiting nutrient availability increased. Soil pH varied between 7.0 and 8.3 in these experiments and was not a significant covariate in these experiments (pW = 0.676, df = 3.00, 875).
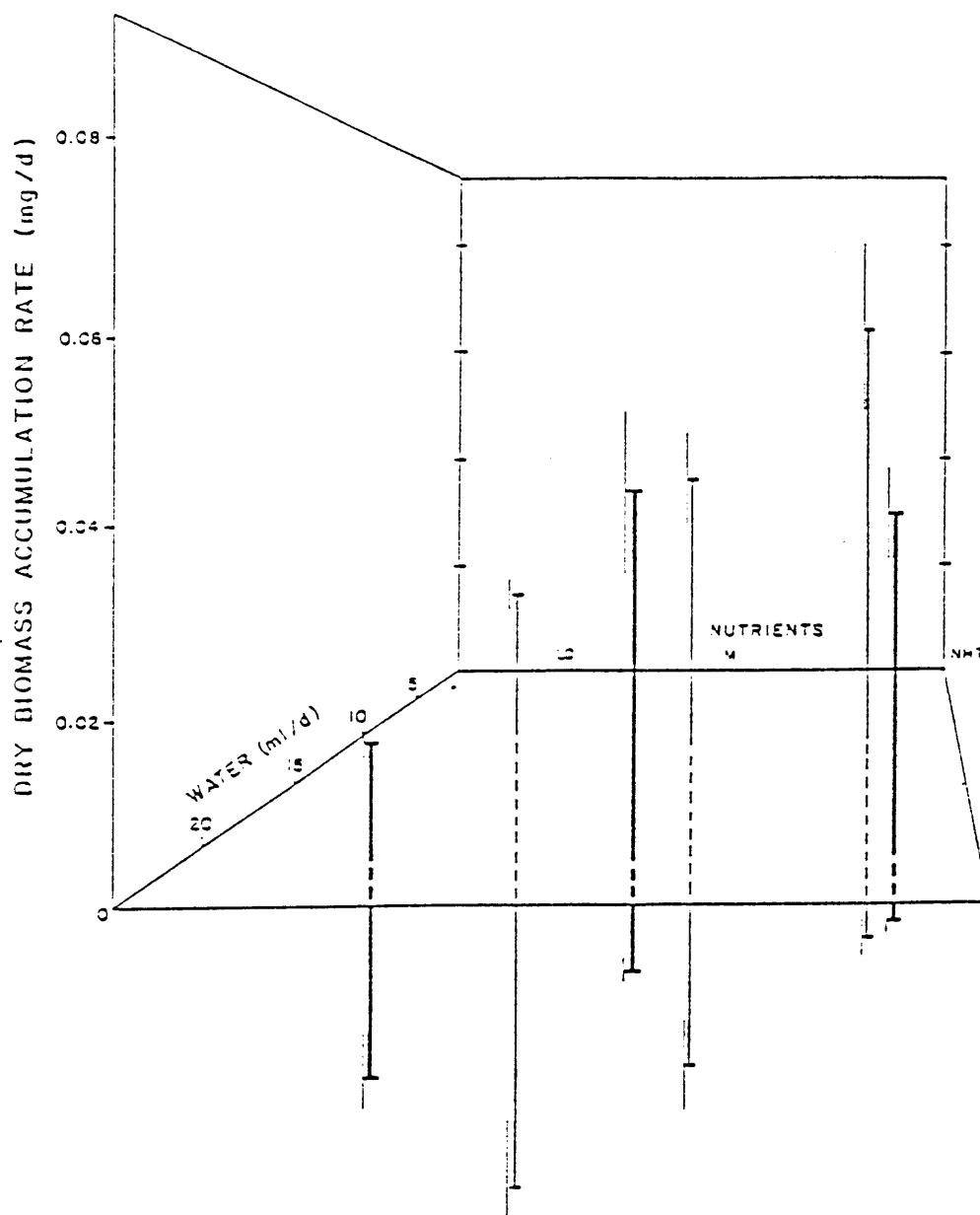
Figure 4.5   Dry biomass accumulation rate of <u>Tamarix ramosissima</u> seedlings grown under 3 levels of nutrients and 2 levels of water for one month in coarse, pre-dam soil for above ground and below ground growth.   Nutrient treatments included: low = distilled water (no nutrients) added to coarse, post-dam soil; medium = 50% Kaufman et al. (1975) solution added with daily water; high = 100% Kaufman solution added with daily water. Error bars are 1 s.e. MANOVA analyses revealed that water availability significantly affected biomass and allocational patterns (FW = 13.012, pW = 0.000, df = 5,48), and nutrient availability significantly influenced relative allocation to roots (FW = 11.264, pW = 0.000, df = 10, 96).   Interaction effects were not significant (pW = 0.202).

Salinity

Seedlings of 4 dominant species responded differentially to experimental salinity gradients which spanned the change in salinity incurred by impoundment in riparian soils (Figure 4.6). Tamarix and Tessaria growth rates increased significantly across a salinity gradient of 0.000 to 0.10 M NaCl (R^2 = 0.670, p < 0.001, df = 1,83 for Tamarix; R^2 = 0.343, p <0.001, df = 1,75 for Tessaria). Neither species displayed allocational changes across the salinity gradient (R^2 < 0.033, p > 0.05 for both species). Total growth rates of B. salicifolia and S. exigua seedlings were not significantly correlated with salinity (R^2 = 0.000, p > 0.05 for both species, df = 1,68 and 1,61, respectively); however, S. exigua allocation to roots increased significantly (R^2 = 0.26.1, p < 0.001) while B. salicifolia allocation decreased significantly (R^2 = 0.176, p < 0.001). This allocational shift for S. exigua was reflected in a marked decrease in above-ground growth at higher salinity levels. Comparison of these regression lines (Zar 1984: 300-302) demonstrated that all growth rates were significantly different between species, while relative allocation did not differ significantly for Tamarix and Tessaria.

Field Test of Water Versus Nutrient Responses

The 3-way analysis of variance of Tamarix and B. salicifolia seedling responses to water and soil types in the field revealed that seedling establishment was conditionally dependent on moisture availability (Figure 4.7). No seedlings established in the low water treatments or in the post-dam (fertilized or not) soils in the medium water treatments. White sand surface temperatures exceeded 60°C during the mid-day hours in these field experiments and pan evaporation rates

A.

REGRESSION EQUATION	R^2	p	df	SIGNIF. OF p
$Y_{Tara} = -0.066+10.30X$	67.0%	0.000	1,33	***
$Y_{Tese} = 0.039+6.350X$	34.3%	0.000	1,75	***
$Y_{Basi} = 0.292-0.234X$	0.0%	0.109	1,68	NSD
$Y_{Saex} = 0.282-1.40X$	0.0%	0.500	1,61	NSD

DRY BIOMASS ACCUMULATION RATE (mg/d) vs NaCl CONCENTRATION (M)

Tamarix[a]
Tessaria[b]
Baccharis[cd]
Salix[d]

B.

REGRESSION EQUATION	R^2	p	df	SIGNIF. OF p
$Y_{Tara} = 0.554+1.21X$	3.2%	0.100	1,33	NSD
$Y_{Tese} = 0.645-1.18X$	2.2%	0.200	1,75	NSD
$Y_{Basi} = 0.759-1.97X$	17.6%	0.000	1,68	***
$Y_{Saex} = 0.511+7.04X$	26.1%	0.000	1,61	***

DRY ROOT:TOTAL BIOMASS RATIO vs NaCl CONCENTRATION (M)

Salix[c]
Tessaria[a]
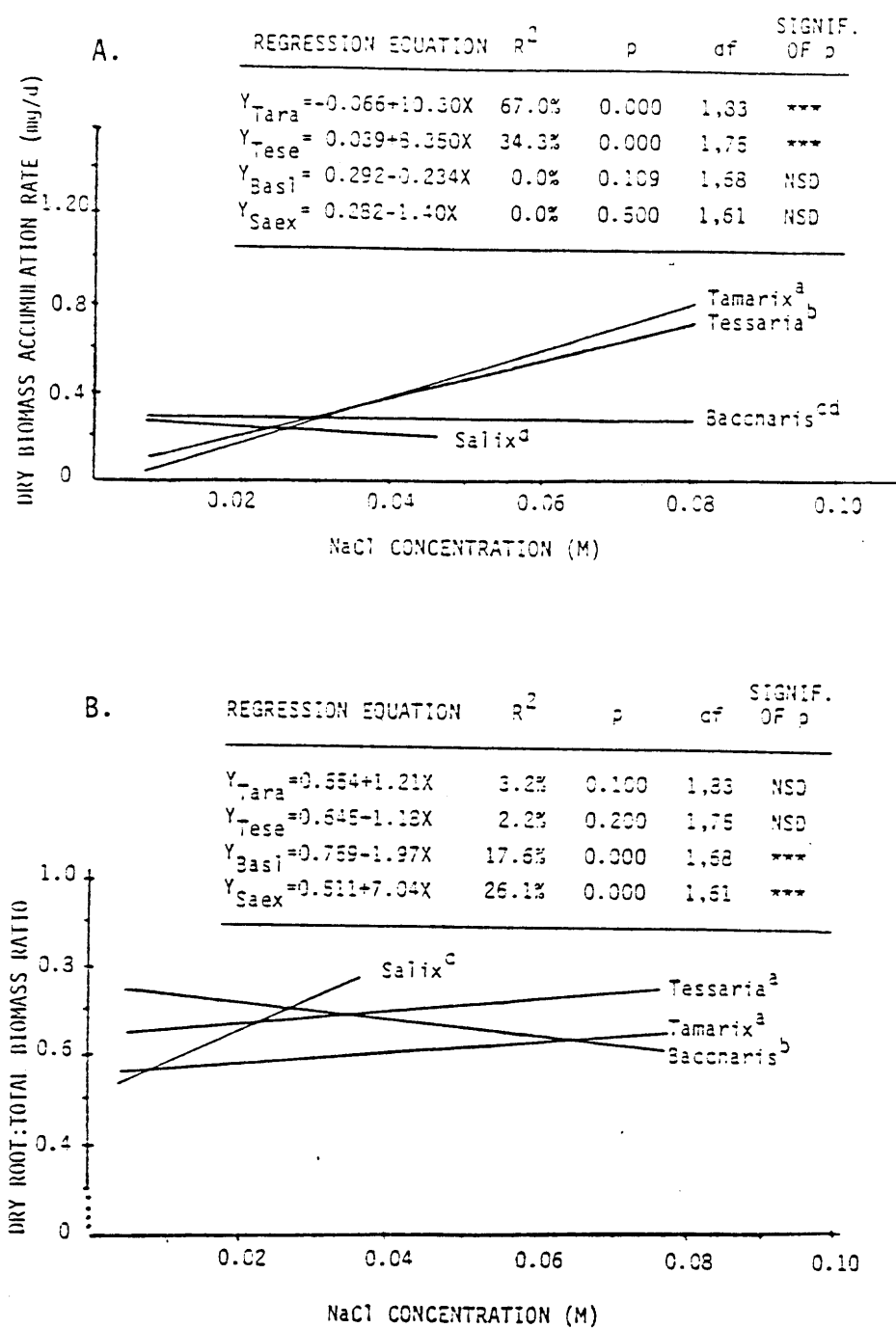Tamarix[a]
Baccharis[b]

Figure 4.6: Dry biomass accumulation rate (BAR) and dry root:total biomass ratio for 4 species of common riparian perennials grown across a salinity gradient spanning pre-dam to post-dam soil salinity levels in the Colorado River riparian corridor in the Grand Canyon. Dry biomass accumulation rate (A); Dry root:total biomass ratio (B).
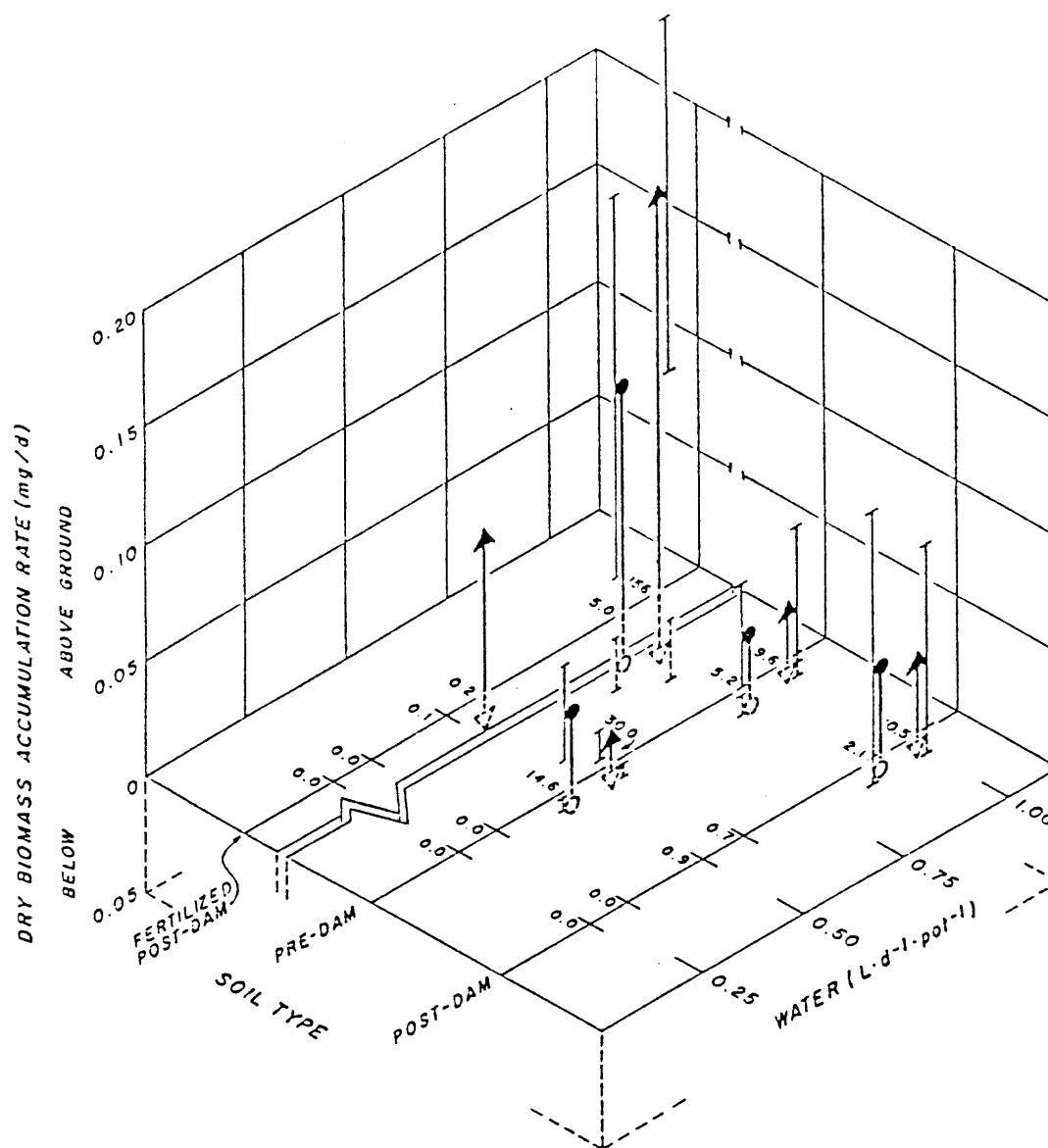
Figure 4.7 Mean percent germination success (numbers on floor) and dry biomass accumulation rate (mg/d) of 40 day old <u>Tamarix</u> <u>ramosissima</u> (circles) and <u>Baccharis</u> <u>salicifolia</u> seedlings (triangles) grown in pre-dam (fine), post-dam (coarse) and fertilized post-dam riparian soils in 12 replicated riverside plots at Lees Ferry, Arizona. Germination success differed between species (pW = 0.012, df= 1,102), water treatments (pW = 0.000, df = 2,102) and soil treatments (pW = 0.000, df = 2,102), with significant interaction between water and soil treatments (pW = 0.000, df = 4,102). Growth rates differed significantly between species, water and soil treatments (pW = 0.000, df = 5,45 for all), and significant interactions occurred between species x soil (pW = 0.000, 10,90) and species x water (p = 0.028, df =5,45).

exceeded 2.0m/yr at Lees Ferry, and seedlings were unable to cope with extreme desiccation stress. Establishment occurred only in the intermediate water treatment in pre-dam soil and in all high water treatments, and establishment success varied significantly between soil types, water and species. Arcsine-transformed (percent germination)$^{1/2}$ varied significantly between species, soil and water treatments, and significant interaction effects existed between water and soil treatments. Baccharis germination was significantly greater than Tamarix (F_W = 6.494, p_W = 0.012, df = 1,102) and germination was significantly influenced by moisture (F_W = 21.174, p_W = 0.000, df = 2,102) and soil type (F_W = 22.826, p_W = 0.000, df = 2,102). Significant interaction effects occurred between water and soil types (F_W = 14.308, p = 0.000, df=4,102). MANOVA analyses of growth rates also revealed significantly faster growth in the high water treatment (F_W = 6.148, p_W = 0.000, df = 5,45) in fertilized post-dam soil (F_W=5.772, p_W = 0.000, df = 10,90), and that Baccharis grew significantly faster than Tamarix (F_W = 91.749, p_W = 0.000, df = 5,45), with significant interaction between soil type and species (F_W = 6.558, p_W = 0.000, df = 10,90) and between water and species (F_W = 2.796, p_W = 0.028, df = 5,45). Seedling growth occurred in pre-dam soil at medium water treatments; however, saturation and apparent water-logging of pre-dam soil retarded seedling growth.

Thus at high water levels, the better aerated post-dam soil provided an improved substrate for seedling growth, with maximum growth under high nutrient conditions. This field experiment confirmed patterns observed in laboratory experiments and revealed that seedlings of both species'seedlings responded primarily to water availability,

which was a function of soil texture, and secondarily to nutrient availability.

Discussion

Dam-induced edaphic changes increased the severity of the selection regime for seedings in the Colorado River corridor in Grand Canyon, reducing the availability of "safe" germination sites. Dominant riparian perennial species in this system required moist, silt-rich substrates for establishment, conditions which were subject to disruption by the discharge regime imposed by Glen Canyon Dam. Most recruitment was observed in silt, virtually no seedling establishment occurred in sand, and seedling densities were low in coarser substrates. Clonally growing species (e.g. Salix exigua, Tessaria sericea, Aster spinosus, Alhagi camelorum) dominated sand beaches which could not be colonized by seed-reproducing species (e.g. Tamarix ramosissima, Baccharis spp., Haplopappus acredenius and Brickellia longifolia; Stevens and Waring 1988). In the field, discharge commonly fluctuated between $100m^3$/sec and $900m^3$/sec according to hydroelectric power demands, inundating and dewatering potential "safe sites" on a daily basis. This was far too brief an interval for seedling establishment to take place. Also, root elongation rates decreased in post-dam soil from 10% for Tamarix to more than 50% for Baccharis sarothroides, delays that would reduce the physical anchoring and nutrient acquisition benefits of roots in the tidal riverside environment.

Soil changes with significant impact on recruitment included decreased water holding capacity, nutrient status and salinity, and increased erodibility of post-dam soils, as compared to pre-dam soils.

Although all species' seedlings were capable of surviving in post-dam sand under laboratory conditions, seedling growth rates were generally greatly reduced in post-dam soils. Field experiments confirmed that germination, seedling growth and survivorship were limited by moisture and nutrient availability, and moisture interactions with substrate particle size. Establishment only occurred in pre-dam silt under a moderate moisture regime, but in all substrates having abundant water in these experiments. Field seedling growth rates in the saturated post-dam soils were found to be greater than in pre-dam soils, probably in response to the physiological constraints associated with water-logging in the pre-dam silts.

Seedling allocational responses to altered edaphic conditions varied significantly between species and between soil types. For example, root:total allocation generally decreased in higher quality soils and up to a threshold of moisture availability. Although soil saturation decreased growth rates of Tamarix and B. salicifolia, low moisture and nutrient availability increased relative allocation to roots. Greater API was positively correlated with seedling abundance in this system. Selection against species with low phenotypic plasticity, such as Populus fremontii, Prosopis glandulosa, Acacia greggi and Fallugia paradoxa, has increased, and clonal and phenotypically plastic species have enjoyed a selective advantage. Phenotypic modulation of seedling architecture varied consistently within species and had a significant adaptive value in this unpredictable riparian environment (Smith-Gill 1983; Lively 1986; Schlichting 1986).

These results indicated a textural and chemical basis for the rapid vegetational change in this system. Nutrient requirements varied

between species: Tamarix seedlings responded positively to increased nitrogen availability; S. exigua seedlings required potassium and micronutrients; while B salicifolia and Tessaria sericea required a combination of phosphate, nitrogen and other minerals for maximal growth. Usable nitrogenous compounds were relatively rare in the post-dam riparian corridor because of reduced allochthonous input associated with impoundment and limited decomposition in the arid environment (Stevens and Waring 1988). Nitrogen concentrations were highest at the soil surface under the canopies of mature plants, where T. ramosissima seedlings never occurred, but where S. exigua and Tessaria clonal ramets arose and where Baccharis spp., a relatively shade tolerant genus, occasionally germinated. Soil pH did not appear to influence recruitment; however, decreasing soil salinity in post-dam substrates may have reduced recruitment success of Tamarix and, to a lesser extent, Tessaria, whose seedling growth rates were positively correlated across the range of soil salinity spanning the pre-dam to post-dam era. Allocational patterns of S. exigua and B. salicifolia demonstrated that these species' growth was poorly or negatively correlated with salinity. Decreased soil salinity in post-dam soil improved substrate conditions for Salix and Baccharis while substrate conditions for Tamarix and, to a lesser extent, Tessaria deterioriated, placing the latter two species at a selective disadvantage. The ecologically deleterious effects of dam-induced soil changes have been more severe for Tamarix recruitment than for Tessaria because Tamarix seeds are short-lived and its seedlings were the slowest growing of all species tested, while Tessaria was a clonal species and exhibited rapid seedling growth. Thus decreased soil nutrient concentrations and salinity in

coarse, post-dam soils have differentially affected recruitment of the dominant riparian species in this system, and these factors have been responsible for the reduced recruitment success and consequent displacement of Tamarix in coarse sand soils. If aggradation of tributary sediments (fine, nutrient- rich deposits) occurred, the recruitment success of Tamarix would be improved.

Stream regulation is one of the most common forms of anthropogenic disturbance in riparian systems; yet, if properly managed, dams may be used to augment and even improve riparian habitats in downstream reaches, and thereby repay for habitat losses upstream. Largely by accident, large dams enhance riparian habitat conditions in downstream reaches, but unconcerned management reduces the potential productivity of that habitat. Under discharge regimes that prevent aggradation of tributary sediments, "safe site" availability will continue to decrease, further reducing recruitment. Managers should recognize that dam operating criteria can be adjusted to maximize both ecological and economic benefits of large dams (Water Science and Technology Board 1987).

CHAPTER 5

CONCLUSIONS

The structure and development of riparian plant communities in the Grand Canyon was influenced by abiotic moisture, disturbance, exposure and substrate gradients and by adaptation of constituent species to those critical gradients, but was little affected by interactive biotic factors. Flooding disturbance effects were conditionally dependent on moisture availability, with opposite community responses (species richness, density and/or basal cover) in perennial as compared to intermittent tributaries. Riparian plant community structure was strongly influenced by differential adaptation and the "gradient/adaptation" hypothesis was supported by the data gathered here because xerophytes and riparian phreatophytes demonstrated significant adaptation to the moisture and disturbance regimes that characterized their niches.

Direct forms of interspecific competition were apparently rare and ineffectual regulators of riparian plant community structure as compared to abiotic regulatory mechanisms. Evidence suggesting a regulatory role for direct interspecific competition was found only under rarely encountered conditions of ecological stability, such as at spring sources. Given that the occurrence of interspecific competition was conditionally dependent on both moisture availability and ecological stability, I hypothesized that the pattern of successional displacement of exotic _Tamarix ramosissima_ by _Salix exigua_ in the dam-controlled

Colorado River riparian corridor could be attributed to direct interspecific competition. This hypothesis was experimentally tested at three life history stages between these two dominant species and supported only at the seedling stage, where Tamarix was strongly outcompeted by Salix. However, Salix seedlings were extremely rare in the field, limiting the significance of that interaction. Indirect, preemptive forms of competition strongly reduced the potential for seedling establishment, including soil hydrophobitization, duff accumulation and shading. These indirect competitive mechanisms exerted a stronger influence beneath Tamarix canopies than beneath Salix.

Other interactive biotic mechanisms were examined in this system. Comparative herbivory studies between these two species indicated that herbivory was likewise unimportant as a driving mechanism in their successional interaction (Stevens 1985). Mutualistic associations were not directly examined in this study but preliminary experiments on seedling growth in sterilized versus unsterilized field soils demonstrated no significant effect on seedling growth (Stevens unpublished data). Therefore fugal associations were not anticipated as being of overtly influential in the successional process.

The pattern of successional displacement of Tamarix by Salix in the dam-regulated Colorado River corridor was therefore attributed to several abiotic mechanisms. Analysis of dam-induced soil changes revealed that daily river "tides" created by hydroelectric power production resulted in erosion of fine sediments at the water's edge where seedling establishment was most likely. Increasing coarseness of fluvial substrates resulted in decreased water holding capacity and reduced nutrient availability. These changes reduced "safe" germination

site availability for riparian plant species, and reduced seedling survivorship and growth. Significant between-species differences were found for growth rates in pre-dam versus post-dam soil, and to limiting nutrients and decreasing soil salinity. The consequences of these soil changes included: 1) increased selection against species with low phenotypic plasticity and short-lived propagules; and 2) differential colonization success of species with clonal growth strategies (e.g. Salix exigua, Aster spinosus, Tessaria sericea and exotic Alhagi camelorum) over non-clonal shrub and tree species.

These results, coupled with those of competition studies, suggested that successional displacement of Tamarix by Salix in the dam-controlled Colorado River corridor was best described as "failing inhibition" for Tamarix and "tolerance" on the part of Salix. Tamarix preemption of space on terraces not subject to post-dam flooding has begun to decrease because of non-self-replacement. Salix has expanded into habitats dominated by Tamarix through its clonal growth strategy and greater tolerance of shade.

The future of riparian habitat in the dam-controlled river corridor relies on discharge managment practices at Glen Canyon Dam. After 25 years of relative ecological stability through discharge regulation, river corridor vegetation structure resembled that of intermittent tributaries but with greater dominance of exotic Tamarix ramosissima. Under an ecologically stable hydrologic regime a significant amount of time will be required for Colorado River riparian vegetation to begin to resemble that of perennial tributaries. Discharge management may be used to facilitate riparian vegetation development in the Grand Canyon (Stevens and Waring 1988). The value of the riparian habitat, native

and exotic fisheries, and hydroelectic power generation and recreation is great in this system, and the Bureau of Reclamation is presently conducting studies on the adequacy of existing dam management criteria. Political decisions resulting from these studies will determine the extent and composition of future riparian vegetation in this system.

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